

National Park Service
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National Capital Region
Washington, DC



Amphibian Monitoring in the National Capital Region: A focus on lentic and lotic habitats

Natural Resource Report NPS/NCRN—2008/088



ON THE COVER

Ambystoma maculatum(spotted salamander)

Photograph: courtesy of the U.S. Geological Survey, Northeast Amphibian Research and Monitoring Initiative

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Amphibian Monitoring in the National Capital Region: A focus on lentic and lotic habitats

Natural Resource Report *NPS/NCRN/NRTR—2007/001*.

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January 2008

U.S. Department of the Interior
National Park Service
National Capital Region Network
Center for Urban Ecology
Washington, DC

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Please cite this publication as:

Mattfeldt, S. D., E. H. C. Grant, and L. L. Bailey. 2008. Amphibian Monitoring in the National Capital Region: A focus on lentic and lotic habitats. Natural Resource Technical Report. Natural Resource Report *NPS/NCRN/NRTR—2008/088*. National Park Service, Center for Urban Ecology, National Capital Region, Washington, DC.

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Abstract

This report describes ongoing amphibian monitoring efforts in the National Capital Region Network. Amphibian monitoring was initiated in 2005 and is currently concentrated in Chesapeake and Ohio Canal National Historic Park and Rock Creek Park, with stream (lotic) sampling also occurring in Prince William Forest Park. The objectives of the monitoring program are to develop an efficient long-term sampling design to: (1) describe the current distribution of amphibians and explore factors that may influence occupancy probabilities or distributional patterns, (2) determine if amphibian distributions are changing annually, and if so, explore whether occupancy changes are related to habitat variables and (3) provide information to aid in generating and testing hypotheses that differentiate among possible causes of long-term changes in the proportion of area occupied among species, habitats, and park areas. Here, we present analysis from 2005-2007 and describe our findings related to the first two objectives. We discuss our results in the context of the National Capital Region's continuing amphibian monitoring program.

We detected 13 amphibian species in each year of sampling 33 wetlands from the Potomac Gorge area within Chesapeake and Ohio Canal National Historic Park (CHOH). We found that detection probabilities were less than one and were related to water temperature or survey visit for most species. Initial occupancy estimates (ψ_{2005}) ranged from 0.15 ± 0.06 ($\psi \pm 1\text{SE}$) for *N. viridescens* to 0.68 ± 0.09 for *R. clamitans* based on a model with constant initial occupancy, colonization, and extinction probabilities. All of the environmental and habitat covariates influenced initial occupancy estimates for one or more species, especially wetland hydroperiod. Hydroperiod was an important variable in initial occupancy estimates for seven of the eight species analyzed and in all cases, the influence was positive. This finding suggests that wetland hydroperiod is likely a limiting factor in determining the distribution of many of the wetland breeding amphibians found at CHOH. In addition to hydroperiod, wetland area and flooding potential also influence occupancy probabilities for some lentic amphibians. This is the only study we know of that demonstrates the negative influence that flooding may have on the probability of occupancy for two amphibian species: *A. maculatum* and *R. sylvatica*. The remaining covariates we explored influenced the occupancy probabilities of some species (e.g., Percentage canopy cover for *P. crucifer* and *R. clamitans*), but the relationships were not consistent among species, nor with our *a priori* hypothesis.

While derived year-specific occupancy estimates for lentic amphibian species were relatively constant over the three years, the occupancy state did change among sites for most species (i.e., there was local turnover at sampled wetlands). Some sites were colonized and others failed to support breeding and/or foraging activity (i.e., became "unoccupied"). Though most colonization and extinction estimates were constant over time (years) and space (among wetlands), there was one notable exception: local extinction probabilities for *R. clamitans* were lower for wetlands with longer hydroperiods. It is important to note that these results are based on only two estimates of the rate parameters (colonization and extinction probabilities), and future data may reveal more information on the factors influencing turnover in local wetland occupancy. Given our relatively small sample size and our findings from exploring sampling design trade-offs it will likely

require more than five years of data to discern factors that influence rate parameters for lentic amphibian species.

We observed four species of stream salamanders in each year of our study: *Desmognathus fuscus*, *Eurycea bislineata*, *E. longicauda*, and *Pseudotriton ruber*. Detection probabilities varied among these species and years. There was considerable uncertainty in terms of variables influencing occupancy probabilities and rate parameters for the 3 species analyzed. In general, initial occupancy estimates were higher for stream transects in CHOH compared to ROCR, except for *E. bislineata* which had high occupancy probabilities in both parks. *Desmognathus fuscus* and *P. ruber* had higher occupancy probabilities at transects near the stream headwaters, but our *a priori* hypothesis that proximity of the stream origin to the park boundary or road would result in lower occupancy probabilities was not well supported for any of the 3 species. We expected models specifying no turnover (i.e., $\gamma = \epsilon = 0$) to be among the top models for all species, but this was not the case. While stream communities changed little among the 3 years study, models where colonization probabilities included the ‘network’ covariate were among many of the top models for *P. ruber*, suggesting the potential for higher colonization probability in stream networks with a confluent first order branch. As with our lentic sampling, more years of data, encompassing both wet and dry years, are needed to further elucidate the potential relationship between spatial covariates and site occupancy and related rate parameters for stream salamander species.

Introduction

The National Capital Region Network has identified amphibians as a priority taxonomic group for its Inventory and Monitoring program. The goals of this program are to document at least 90% of the amphibian species in its parks, and to determine whether the integrity and status of amphibian populations are changing over time. As of 2004, all of the parks had completed amphibian inventories (Shawn Carter, National Park Service, *personal communication*), and planning for monitoring efforts were initiated. The objectives of the monitoring program are to develop an efficient long-term sampling design, in cooperation with park service biologists and managers, to: (1) describe the current distribution of amphibians (i.e., estimate initial occupancy probabilities for targeted species) and explore factors that may influence occupancy probabilities or distributional patterns, (2) determine if amphibian distributions are changing annually, and if so, explore whether occupancy changes are related to habitat quality, paying special attention to factors associated with increased urbanization in the region, and (3) provide information to aid in the generating and testing of hypotheses that differentiate among possible causes of long-term changes in the proportion of area occupied among species, habitats, and park areas.

In 2005 a pilot study was initiated by U.S. Geological Survey's Northeast Amphibian Research and Monitoring (USGS, NEARMI) personnel to collect detection/nondetection data for amphibians located in terrestrial, lotic (stream) and lentic (wetland) habitats at two parks in the National Capital Region Network (Chesapeake and Ohio Canal National Historic Park, Rock Creek Park). Multiple survey techniques were employed and data from each survey method was analyzed by USGS NEARMI researchers and evaluated by both USGS and NPS personnel (see Amphibian Monitoring Protocol for the National Capital Region Parks 2006, 2007). Based on this evaluation, a decision was made to focus monitoring efforts on amphibians that occupy lentic and lotic habitats (Amphibian Monitoring Protocol for the National Capital Region Parks 2006, 2007).

This report details these ongoing monitoring efforts, describes findings based on analysis of the current available data (2005-2007), and considers modifications and recommendations of future long-term sampling needs and designs.

Methods

Our study focused on wetlands (lentic habitat) and first-order streams (lotic habitat) in the Chesapeake & Ohio Canal National Historical Park (CHOH: 38° 59'N, 77° 14'W), and lotic habitats only in Rock Creek National Park (ROCR) and Prince William Forest Park (PRWI). Both CHOH and ROCR are located within the urbanized Washington DC metropolitan area, and PRWI is located near Triangle, Virginia. Our study at CHOH was conducted in the urbanized, southern section of the park, known as the Potomac Gorge area (Figure 1), while the studies at ROCR and PRWI involved a random sub-sample of all mapped first-order streams (e.g., Figure 2).

Lentic Habitats

Site Selection

Our sample frame consisted of all known (mapped) wetlands in the Potomac Gorge area of CHOH. For the purposes of this study we limit wetlands to those that are isolated, palustrine, and less than 0.4 hectare in area. These constraints are based primarily on sampling logistics, but also reflect lentic amphibian's primary breeding habitats. Our sample frame consisted of 169 wetlands of which we selected a random sub-sample of 33 wetlands (Table 1).

Field Methods

The 33 wetlands were visited on four occasions from March-July for three years (2005-2007; 12 visits over the study duration). Two detection methods were used to document the presence of amphibian species during these visits: visual encounter or dip-net surveys. We conducted visual encounter surveys early in the year to target amphibian egg masses and breeding adults. Observers walked along the perimeter of the wetland, recording all life phases of amphibian species observed in the wetland, or under terrestrial cover (>6 cm) within a meter of the wetland edge. Dip-net surveys were conducted later in the season to target larval amphibians. Every sampling visit was conducted by two independent observers: observers began their surveys at opposite sides of a wetland site, navigated around the pond in the same direction, and did not communicate during the survey.

During each visit to a wetland we measured several habitat covariates likely to influence amphibian occupancy and/or detection including: water temperature, conductivity, percent canopy cover, aquatic vegetation, water depth, and the wetland area (Table 2, also see Amphibian Monitoring Protocol for the National Capital Region Parks 2007 SOP#5 for more details). Using GIS (ArcMap9, Environmental Systems Research Institute, Redlands, CA) we constructed a relative flood potential index by combining distance and slope from the river: higher values indicate wetlands that were less likely to flood (Table 2). These calculated flood index values corresponded well to the flooding events we observed during the study. Further details of the field methods can be found in Amphibian Monitoring Protocol for the National Capital Region Parks 2007.

Analytical Methods

We used multi-season occupancy models to estimate initial occupancy probabilities (ψ_{2005}) for each species, as well as colonization (γ) and extinction probabilities (ϵ) between years (MacKenzie et al. 2003, 2006). Occupancy probabilities were also derived for 2006 and 2007. These models account for imperfect detection, and provide unbiased estimates of occupancy, colonization and extinction probabilities, if the model assumptions are met. Specifically, multi-season occupancy models assume that: (1) a species occupancy state at each site does not change over surveys within a season (i.e., the sites are 'closed' to changes in occupancy within a season), (2) detection of species and detection histories at each location are independent, (3) the target species is never falsely detected, and (4) there is no unmodeled heterogeneity in any of the model parameters (occupancy, colonization, extinction or detection probabilities; MacKenzie et al. 2003, 2006).

To apply these models, detection histories are compiled for each species at each site (wetland). Example detection histories from this study include the following histories from three wetlands sites: 11010000 11000000 111000--. “1” represents detection of the target species during a single observer’s survey, while “0” represents non-detection. Missing values, denoted as ‘–’ represent a wetland or site that was dry, flooded or not visited. There were eight detection/nondetection occasions per year (two observers surveyed each wetland during four visits). We considered the occupancy state of wetlands without standing water to be uncertain, and thus treated visits to dry wetlands as missing values.

A priori, we hypothesized that initial amphibian occupancy may be related to several local habitat variables (e.g., percent canopy cover, hydroperiod, wetland surface area, etc., see Table 3). The influence of the percent canopy cover and aquatic vegetation on the probability of occupancy was expected to vary by species: for *Bufo spp.*, *P. crucifer*, and *R. clamitans* we expected a negative relationship between occupancy probability and the percent canopy cover, and for the other species we expected no relationship between occupancy probability and canopy cover (Skelly et al. 1999). The relationship (positive or negative) between occupancy probability and the other covariates was expected to be consistent among species (although the magnitude of the relationship may vary by species; see Table 3 for a complete list of *a priori* expectation and associated literature).

Using our *a priori* hypothesis we defined a small set of models that might influence initial occupancy probabilities (ψ_{2005}) for each of the 8 amphibian species (Table 4). We considered hydroperiod and wetland area to be primary factors influencing the probability of amphibian occupancy. Flood index, conductivity, aquatic vegetation, and canopy cover were considered secondary factors. Our candidate model set (Table 4) was designed to compare the relative importance of the variable within each set of factors (primary or secondary), but not between these sets.

Since the occupancy state may have changed over the three years, we estimated colonization and extinction probabilities (also referred to as rate parameters). We expected larger wetlands to have a higher probability of colonization for *A. maculatum*; and we expected wetlands with a shorter hydroperiod to have a higher probability of extinction for *A. maculatum*, *P. crucifer*, *R. catesbeiana*, *R. clamitans* and *R. sylvatica*. In addition, we investigated whether colonization or extinction probabilities were zero, varied by year, or were constant among years.

We composed candidate models using occupancy structures denoted in Table 4, rate parameter structures described in the previous paragraph, and detection probability (p) structures that modeled p as a function of water temperature (linear or quadratic), maximum water depth, or survey visit with an additive year affect. Water temperature is likely to influence the probability of detection through its influence on amphibian activity and egg/tadpole development, and may also function as a surrogate for breeding phenology. Amphibians may be more difficult to see or capture in deeper wetlands.

Analyses were performed using program PRESENCE (Hines and MacKenzie 2004) or Program MARK (White and Burnham 1999). These programs use Akaike’s Information Criterion (AIC) to rank models and calculate Akaike weights (w) (Burnham and Anderson

2002). We evaluated the relative importance of the variables by summing the AIC weights for all models in the model set where variable j occurred ($w_+(j)$; Burnham and Anderson 2002).

Exploring sampling design trade-offs: Using data from the first three years of monitoring as pilot information we explore sampling design trade-offs under a specified monitoring objective: in this case, to detect change in amphibian population distributions (Amphibian Monitoring Protocol for the National Capital Region Parks 2006, 2007, Bailey et al. 2007). We chose two species (*A. maculatum* and *N. viridescens*) that are likely to be sensitive to urbanization, but whose response may vary due to their differing initial occupancy probabilities, habitat requirements, dispersal distances, and extinction and colonization probabilities (Shoop 1974, Healy 1975, Gill 1978, Gibbs 1998; Rubbo and Kiesecker 2005).

We explored the ability of four long-term sampling designs to detect change in amphibian occupancy and distribution by simulating four different change scenarios (Tables 5 and 9). The first two scenarios estimate the power of each design to detect change in occupancy for a species that incurs a 50% decline in occupancy over five years. This level of decline was generated using the species initial occupancy estimates (ψ_{2005}) with either: (scenario 1) constant extinction and colonization probabilities (referred to collectively as ‘rate parameters’), or (scenario 2) rate parameters that fluctuated between good (higher colonization and lower extinction probabilities) and bad years (lower colonization and higher extinction probabilities; Table 5). A third scenario examined the power of the various sampling designs to detect occupancy change for species with a 50% increase in occupancy over five years assuming constant rate parameters. The fourth and final scenario looked at the power to detect time-specific rate parameters (γ_t, ϵ_t) for species whose distribution changes among occupied wetlands but whose overall occupancy probability remains the same over time (Table 5). For *A. maculatum*, our initial analysis showed higher occupancy probabilities for wetlands that retained water through at least 2 survey seasons (Amphibian Monitoring Protocol for the National Capital Region Parks 2007, SOP#5), thus for this species we considered two groups of sites: Long Hydroperiod wetlands and Short Hydroperiod wetlands with an approximately equal number of wetlands (sites) in each group. For *N. viridescens* we only examined the first scenario, since the initial analysis revealed low occupancy probabilities ($\hat{\psi}_{2005}=0.15$) and constant rate parameters (Table 6). For each of the four change scenarios, we examined the influence of four sample designs by varying the number of sampled wetland sites (35 or 70) and the frequency of surveys (annually or alternate years; Table 5).

To determine whether the sample design affected the ability to detect a change in amphibian distributions, we used a likelihood ratio test to approximate power (Burnham et al. 1987:214-217). In each case the scenarios described above (Table 5) were considered the “true” generating model, or the alternative hypothesis (H_a : time-specific occupancy estimates), and the null hypothesis was represented by models representing no change in occupancy or its related rate parameters (H_0 : time-constant occupancy and/or rate parameters). We approximated power (assuming $\alpha=0.05$ or $\alpha=0.10$) by using the resulting chi-square statistic as the noncentrality parameter, λ , and calculating power from a non-

central chi-squared distribution (Burnham et al. 1987; Devineau et al. 2006; Bailey et al. 2007). All data generation was performed using program GENPRES (Bailey et al. 2007) and analyzes were performed using Program MARK (White and Burnham 1999).

Lotic Habitats

Site Selection

Streams were chosen from all known headwater, 1st order streams in each of three parks in the National Capital Region Network [Chesapeake and Ohio Canal (CHOH), Rock Creek (ROCR) and Prince William Park (PRWI)]. Based on GIS-mapped streams (provided in digital form by NPS for CHOH and PRWI and mapped in the field in 2005 for ROCR), streams were classified as having confluent first order streams of at least 150 m in length ('branched'), or having a single 1st order branch ('unbranched') before meeting a higher order stream. We then attempted to randomly select an equal number of branched and unbranched streams from the set of mapped streams from each park; field surveys revealed that only CHOH and PRWI had branched streams according to our definition. Seven streams were randomly chosen at CHOH (Figure 1), five streams at ROCR (Figure 2), and 53 streams at PRWI. We surveyed PRWI streams in 2006, and at that time only 19 streams had sufficient surface water flow to warrant sampling for stream salamanders. Data from PRWI is not included in the multi-season analysis presented here, but with additional years of sampling, a similar analysis will be performed including the PRWI data.

Field Methods

We surveyed streams for salamanders in the genera *Desmognathus*, *Eurycea*, and *Pseudotriton*. Each stream was surveyed using two pairs of 15x3 m transects (surveying 2 m on the bank and 1 m in the water). The first transect pair was located at the stream origin, with the second pair located 100 m from the end of the first pair along the same stream (145 m from the stream origin). Each pair of transects (i.e., a 'site') was visited twice (once each in June and July) by two observers. We found that searching the leaf litter along with turning cover objects (e.g., rocks and logs) is suitable for detecting larval *P. ruber*, which has a low detection probability when turning cover alone (Mattfeldt and Grant 2007). We included detections of larval *P. ruber* from 2005 leaf litterbag surveys in the analysis presented here: surveys in 2006 and 2007 incorporate leaf litter searches every 0.5 m along the transect, in addition to turning cover objects (see Amphibian Monitoring Protocol for the National Capital Region Parks 2007 SOP#6 for details). We conducted two passes of each transect on each visit, and summed the detections for our analysis.

For each site, we recorded several covariates that were likely to influence stream salamander occupancy and rate parameter probabilities including: transect location (distinguishing whether the transect pair was located at the stream origin or not), park (CHOH or ROCR), whether or not the stream was branched, and whether the stream was within 100m of the park boundary or internal park road (candidate model set in Table 7).

Analytical Methods

We performed our analyses for three species, *Desmognathus fuscus*, *Eurycea bislineata* and *Pseudotriton ruber*. We use the multi-season modeling approach of MacKenzie et al. (2003, 2006) and analyzed species-specific data from 26 paired transects on 12 streams (seven streams at CHOH and five streams at ROCR) from 2005 – 2007. Each year was considered a 'season', with two sampling occasions (June and July) within each season. We

assumed that each site was closed to changes in occupancy within a season (i.e., no local colonization or extinction of a species), but we investigated the possibility of local colonization or extinction between seasons (years). We focused on four covariates we hypothesized would affect occupancy (ψ), colonization (γ) or extinction (ϵ). See Table 7 for candidate models list.

A priori, we expected initial occupancy of paired transects in 2005 (ψ_{2005}) to be a function of the location along the stream, thus we included a categorical covariate which described whether the transect pair was located at the stream origin ('transloc' = 0) or 145 m from the origin (transloc = 1). We also allowed for different initial occupancy at the two parks (covariate 'park'; ROCR = 1, CHOH = 0). In urbanizing systems, streams whose origin begins near the park boundary or near an internal park road may have lower initial occupancy probabilities and be more likely to go extinct, due to factors external to a park, or due to visitor traffic within a park. We therefore included models with a categorical variable for either initial occupancy and/or extinction probabilities ('nrbound' = 1 for transect pairs on streams that originate within 100 m of the park boundary or internal park road, otherwise nrbound = 0; Table 7).

Based on a separate analysis that included data from 43 streams (involving 11 of the streams analyzed here and 32 additional streams from across Virginia), we found that occupancy of stream salamanders may be positively related to the presence of a confluent, 1st order stream (EHC Grant and LE Green, unpublished manuscript). The presence of a confluent branch may allow for increased colonization rates (Lowe and Bolger 2002, Grant et al. 2007), and therefore we expected a positive relationship between colonization probability and a categorical variable 'network' (network=1 if a stream is branched or confluent with another first order stream, network=0 if a stream is unbranched). We suggest caution in interpreting the network covariate here, as all branched streams were located in CHOH, thus potentially confounding the effect of network and park. Incorporating data from other parks (i.e., PRWI) in the future may improve the interpretation of this covariate in future multi-season analysis.

In addition, to the above model structures involving covariates, we also investigated whether γ or ϵ were zero, nonzero but constant over years, or varied by year. We expected *a priori* that models with no colonization or extinction (i.e., $\gamma = \epsilon = 0$) to have the most support, given assumptions of population stability of stream salamanders in natural ecosystems by previous authors (e.g., Davic and Welsh 2004, Hairston et al. 1993), however if rate parameters were non-zero, we expected models with the covariate relationships described above to be supported (Table 7).

Finally, using the most general occupancy and rate parameter structure for each species (i.e., the model with the most parameters), we investigated three different detection probability, p , structures: (1) p differ by year, (2) p differ among months (June vs. July), and (3) an additive effect of month and year. For those models that converged, we found that modeling detection as a function of month for *D. fuscus*, and year for *P. ruber* and *E. bislineata*, consistently resulted in higher ranking (lower AIC) models than other detection probability structures. Therefore, we used p (month) for *D. fuscus* and p (year) for *P. ruber*

and *E. bislineata*, when fitting models with various occupancy and rate parameters. We verified that our choice of covariates on p did not affect inference regarding occupancy and rate parameters by fitting the top models with all the 3 detection structures originally considered: p (month), p (year), and p (year+month). These models were typically lower ranked and the estimates of the parameters of interest (ψ_{2005} , ϵ , γ) did not differ markedly with different structures on p (see Results section below).

Results

Lentic Habitats

We detected the same 13 amphibian species in all years of the lentic study: *A. maculatum*, *A. opacum*, *Bufo americanus*, *B. fowleri*, *Hemidactylium scutatum*, *Hyla chrysoscelis/versicolor*, *N. viridescens*, *Pseudacris crucifer*, *Rana catesbeiana*, *R. clamitans*, *R. palustris*, *R. sphenoccephala*, and *R. sylvatica*. *A. opacum*, *Hemidactylium scutatum*, *Hyla chrysoscelis/versicolor*, and *R. sphenoccephala* were rarely observed and did not have sufficient detections for formal occupancy analysis. *B. americanus* and *B. fowleri* tadpoles are very similar in appearance and were treated as a *Bufo spp.* complex.

Detection probabilities, p , were related to water temperature or survey visit for most species. *R. catesbeiana*, *R. clamitans* and *R. palustris* all showed a quadratic relationship between water temperature and detection probability, with an optimal temperature likely occurring when these species are most active (Table 6, Figure 3). *A. maculatum*, *P. crucifer*, and *R. sylvatica* had detection probabilities that varied by both visit and year (Table 6). The probability of detecting *A. maculatum* was lower in 2006, relative to 2005 and 2007 (Figure 4).

Initial occupancy estimates (ψ_{2005}) ranged from 0.15 ± 0.06 ($\psi \pm 1\text{SE}$) for *N. viridescens* to 0.68 ± 0.09 for *R. clamitans* based on a model with constant initial occupancy, colonization, extinction probabilities and detection probability varying by survey visit or varying by survey visit with an additive year affect (Table 8). All of the covariates influenced initial occupancy estimates for one or more species, especially wetland hydroperiod (w_+ (hydroperiod) for most species >0.9 ; Table 6). Here we report the covariates included in supported models with Akaike weights >0.10 ($w > 0.10$, Table 6). The influence of the covariates on initial occupancy probabilities should be considered in the context of the covariates range at the Chesapeake and Ohio NHP (Table 2). For *Bufo spp.*, *N. viridescens*, and *R. palustris* there was much model uncertainty, suggesting no clear relationship between initial occupancy probabilities and any of our collected covariates; we present the results of the analysis in Table 6 but refrain from detailed interpretation.

For the primary factors, hydroperiod had more summed Akaike weight than area for all of the species, except *R. sylvatica*; the relationship between both covariates and occupancy matched our *a priori* predictions (preference for longer hydroperiods and larger wetlands; Table 3; Table 6). With regard to the secondary factors considered for *A. maculatum* and *R. sylvatica*: flood had a positive relationship with the probability of occupancy and seemed especially important for *A. maculatum* initial occupancy (w_+ (flood)= 0.99 and 0.54; w_+

(conductivity)= 0.01 and 0.42 for *A. maculatum* and *R. sylvatica*, respectively). For *R. sylvatica* there was also moderate support for a negative relationship between conductivity and the probability of occupancy. *R. catesbeiana* had a higher probability of occupancy in wetlands without aquatic vegetation (<15%). Contrary to our *a priori* predictions *P. crucifer* and *R. clamitans* had a higher probability of occupying wetlands with a higher percent of closed canopy. For both species the relative variable weight for canopy was high (w_+ (canopy)= 0.92 and 0.99 for *P. crucifer* and *R. clamitans*, respectively). There was little evidence of other relationships with the local habitat variables we considered, these variables had a low relative importance values (i.e., $w_+ < 0.09$).

While derived year-specific occupancy estimates were relatively constant over the three years (Table 8), the occupancy state did change among sites for most species (i.e., there was local turnover at sampled wetlands). In other words, some sites were colonized and others failed to support breeding and/or foraging activity (i.e., went locally “extinct”), as evident by non-zero estimates of extinction and colonization probabilities. These rate parameters were often constant among wetlands (i.e., not related to collected covariates) and years. Time or year-specific rate parameters were favored for two species, *A. maculatum* and *R. catesbeiana*, but our *a priori* factor (wetland area) was not important in estimates of local colonization. Wetlands that were prone to drying had a higher extinction probability for *R. clamitans*.

Exploring sampling design trade-offs

Consistent across all scenarios and species, surveying more wetlands increased the power to detect a change in lentic amphibian distributions (Table 9). Surveying annually increased power approximations compared to surveying in alternate years, especially for scenarios in which rate parameters varied among years (Table 9). For *N. viridescens*, the low power to detect occupancy change would suggest that the ability to detect further distributional declines for this species is poor with realistic sample sizes, though it should be noted that the year-specific occupancy estimates are accurate and unbiased.

Lotic Habitats

We observed four species of stream salamanders in each year of our study: *Desmognathus fuscus*, *Eurycea bislineata*, *E. longicauda*, and *Pseudotriton ruber*. We did not encounter *E. longicauda* with enough frequency to include in the formal analysis. Due to the time period of sampling, we did not detect all age classes of all species, though all species were available for detection. Therefore, we combined detections among all age class for our multi-season occupancy analysis of *D. fuscus*, *E. bislineata* and *P. ruber*.

Detection probability for *D. fuscus* was high and relatively consistent between June (estimate from top model, Table 10: $p_{\text{June}} = 0.74 \pm 0.05$) and July (estimate from top model, Table 10: $p_{\text{July}} = 0.72 \pm 0.05$). There was considerable model selection uncertainty for *D. fuscus* (Table 10), with six models having ΔAIC values ≤ 2.0 units of the ‘best’ model. All but one of the top models included the covariate ‘park’, and most models also included transect location (Table 10). Higher occupancy probabilities were associated with streams in CHOH and transects located near the stream headwaters, as well as streams located near

the park boundary or a major internal park road, though models that included ‘nrbound’ had little support (Tables 10 and 11). There were no consistent set of covariates which were related to colonization or extinction probabilities, though estimates across the top model set suggest that colonization is higher than extinction over our short, three-year study (Table 10). The data did not support our *a priori* hypothesis that proximity of the stream origin to the park boundary or internal park road would result in lower occupancy or greater extinction probabilities for stream salamanders. Because of high initial occupancy estimates, the estimates for our rate parameters would suggest little overall change in occupancy over the three years.

Detection probability for *P. ruber* was variable among the years (estimate from top model, Table 10: $\hat{p}_{2005} = 0.45 \pm 1.16$; $\hat{p}_{2006} = 0.62 \pm 1.67$; $\hat{p}_{2007} = 0.31 \pm 1.50$; standard error estimates are suspect for this model). There was considerable model selection uncertainty for *P. ruber* (Table 10), with six models having ΔAIC values ≤ 2.0 units of the ‘best’ model. All top models included the transect location covariate on initial occupancy, and parameter estimates reveal a strong preference for the stream headwaters for this species (Tables 10 and 11). There was little support for occupancy differences among the 2 parks and though models that included the ‘nrbound’ covariate had little support, streams that were further from park boundaries or roads had slightly higher occupancy probabilities compared to streams near park boundaries (Tables 10 and 11). Models where colonization probabilities included the ‘network’ covariate were among many of the top models, suggesting the potential for higher colonization probability in stream networks with a confluent first order branch, consistent with our *a priori* hypothesis. Extinction probability is likely small, as 5 of the top models specified no extinction ($\epsilon = 0$), and the remaining models with any weight (Table 10) provide estimates of a constant extinction probability which are close to zero. As with *D. fuscus*, because of high initial occupancy estimates, the estimates for our rate parameters would suggest little overall change in occupancy over the first three years of this program.

Detection probability for *E. bislineata* was high but variable among years (estimate from top model, Table 10: $\hat{p}_{2005} = 0.49 \pm 0.07$; $\hat{p}_{2006} = 0.68 \pm 0.06$; $\hat{p}_{2007} = 0.74 \pm 0.06$). There was also considerable model selection uncertainty for this species though only two models had ΔAIC values ≤ 2.0 units of the ‘best’ model (Table 10). Supported models included a diverse array of structures on occupancy, though in general this species had high occupancy probabilities across both parks, with a preference for transects in a lower stream position, and streams which originate near a park boundary or internal park road (Tables 10 and 11). There was also considerable uncertainty in covariates related to colonization, and models in the set having 95% of the model weight included both non-zero estimates of colonization and models which specified no colonization (Tables 10). Models with covariates on extinction were similarly uncertain, and no pattern emerged. Because of high initial occupancy estimates (Table 11) and the estimates for our rate parameters, our results suggest little overall change in *E. bislineata* occupancy over the three years (as with *D. fuscus* and *P. ruber*).

Discussion

Lentic Habitats

Hydroperiod is one of the primary local habitat characteristics associated with amphibian presence or species richness (Skelly et al. 1999, Babbitt et al. 2003, Church *in press*). Our analysis indicates the pattern also holds for pond-breeding amphibians found in CHOH: hydroperiod was an important variable in initial occupancy estimates for six of the eight species analyzed (Table 6). In all cases, the influence was positive; suggesting that wetland hydroperiod is a limiting factor in determining the distribution of many of the wetland breeding amphibians found at CHOH. The hydroperiod of a wetland may vary due to changes outside of the park (watershed modifications, water diversion, or global climate change) or changes within the park (i.e., changes in the canal water level). In addition to hydroperiod, wetland area and flooding potential also influence occupancy probabilities for some lentic amphibian. This is the only study we know of that demonstrates the negative influence that flooding may have on the probability of occupancy for two amphibian species: *A. maculatum* and *R. sylvatica* (but see observational evidence of Dorcas et al. 2006). Flooding by the Potomac River decreases occupancy probabilities for these species, which migrate to and from breeding ponds during the spring when flooding is most likely to occur. The remaining covariates we explored influenced occupancy probabilities for some species (e.g., percentage canopy cover for *P. crucifer* and *R. clamitans*), but the relationships were not consistent among species, nor with our *a priori* hypothesis.

We found that detection probability varied within each season for nearly all species, either among visits or according to water temperature. For some species, detection probabilities also varied among years, underscoring the importance of estimating and modeling detection probability to provide unbiased estimates of occupancy, colonization and extinction probabilities for each species.

In the three years of wetland surveys there was only a slight change in overall occupancy probabilities for most species; however, *R. clamitans* and *R. palustris* do show signs of decline (Table 8). All species experienced some annual turnover, indicating that the same sites are not occupied each year. Using only naïve or implicit estimates of occupancy would suggest little change in these wetland systems and would mask important changes in the distribution of these species among wetland sites (MacKenzie et al. 2006). Though most rate parameter estimates were constant over time (years) and space (among wetlands, Table 6), there was one notable exception: local extinction probabilities for *R. clamitans* were lower for wetlands with longer hydroperiods. It is important to note that these results are based on only two estimates of the rate parameters, and future data may reveal more information on the factors influencing turnover in local wetland occupancy. Given our relatively small sample size it will likely require more than five years of data to discern factors that influence rate parameters (Bailey et al. 2007, Mackenzie et al. 2006; Field et al. 2007), as emphasized when we used these estimates in our exploration of sampling design trade-offs.

Sampling design trade-offs

Our exploration of sampling design efficiency under plausible scenarios of change in lentic amphibian distributions showed that the power to detect change in occupancy may vary by species, sampling frequency, and the number of sampled wetlands. For example, in the first scenario (*50% decline in occupancy over five years, assuming time-constant rate parameters (γ , ϵ)*), the power to detect the decline was higher for *A. maculatum* than for *N. viridescens* for all four sampling designs. If rate parameters vary among years, which are evident for some species despite our short study (Table 6), there is tremendous advantage to an annual sampling frequency (Table 9). For rare species with a low occupancy probability such as *N. viridescens*, survey designs should maximize the number of wetlands sampled to increase parameter precision and power (Mackenzie and Royle 2005, this study). Under the current annual sampling frequency, given the limited monitoring dollars, it will be difficult to detect a “statistically significant” change in occupancy for rare species. However, we reemphasize that if model assumptions are met, the estimates of change in occupancy for these species will be unbiased, but time-dependent occupancy models may not be the most parsimonious given the limited number of occupied wetlands. Management decisions may need to be based on criteria other than statistical significance (power) or parameter precision.

If management agencies are unsatisfied with the current study’s ability to detect change in amphibian occupancy and associated rate parameters, we suggest surveying more wetlands or continue monitoring efforts for a longer time period. Currently, 20% of the lentic sites within the Potomac Gorge area of CHOH, are being surveyed. If an increase in the number of sites is not possible, due to logistic or financial constraints, then the management agencies may need to survey for more years before changes in occupancy can be detected based on power approximations or model selection criteria (MacKenzie et al. 2006, p.219-221, Bailey et al. 2007).

Future Directions

Wetland hydrology represents habitat availability for pond-breeding amphibians. It may be beneficial in the future to simultaneously model both habitat availability, then conditional on available habitat, estimate amphibian occupancy probabilities. Developing this type of joint model is a current area of research by USGS scientists and collaborators (J. Nichols USGS and D. MacKenzie Proteus Wildlife Research Consultants, *personal communication*). We anticipate being able to apply these types of models to lentic data collected at CHOH in the near future.

Lotic Habitats

We expected models specifying no turnover (i.e., $\gamma = \epsilon = 0$) to be among the top models (i.e., $\Delta AIC < 2.0$) for all species. This expectation was supported for *P. ruber* where models with $\epsilon = 0$ were among the top models, though colonization probabilities for this species were nonzero. We found little support for our expectation of no turnover for *D. fuscus* and *E. bislineata* as models with $\gamma = 0$ and/or $\epsilon = 0$ had Akaike weights near 0. For *D. fuscus* and *E. bislineata*, there was substantial model uncertainty, and extinction probabilities may be constant, vary by year, or be related to the proximity of the stream to the park boundary

or internal park road. Across the Mid Atlantic region, 2006 and 2007 were abnormally dry years, and may contribute to local extinctions by reducing the amount of suitable habitat available to stream salamander populations. Surprisingly, even during these dry conditions colonization probabilities were not zero, and may be related to the spatial configuration of the stream branches (i.e., the covariate ‘network’). We urge caution in interpreting the effect; however, as all branched streams were found in CHOH, and thus is confounded with park location. For example, an *a posteriori* model for *P. ruber* with an additive effect of PARK and NETWORK suggests that the colonization probabilities of unbranched and branched networks in CHOH were 0.12 ± 0.13 and 0.58 ± 0.45 , respectively. Incorporating data from other branched streams in a balanced design will allow better investigation of the effect of stream spatial layout on the occupancy rate parameters.

More years of data, encompassing both wet and dry years, are needed to further elucidate the potential relationship between spatial covariates and site occupancy and related rate parameters. Models which can incorporate dynamics of habitat availability and occupancy are forthcoming (J. Nichols and D. MacKenzie, *personal communication*).

Future Directions: Lotic habitat

Stream salamander populations are assumed to be stable in undisturbed systems (Hairston et al. 1993), though there is evidence that large scale, permanent land use change may be related to population declines of some stream salamander species (Price et al. 2006). Further, theoretical (e.g., Fagan et al. *in press*) and empirical (Lowe and Bolger 2002) work finds that population stability in stream systems may be related to the complexity of the stream network (i.e., the number and location of intersecting stream reaches). This would suggest that management for populations of animals living in stream networks must be considered at the catchment scale, instead of most historic stream management approaches which focus on the stream reach scale (Hassett et al. 2005). Future investigation within the National Capital Region Network, combined with other research efforts in the Northeastern United States, will allow us to investigate these relationships more fully. Further, as we note for both the lotic and lentic data, additional years of data collection will allow us to improve these estimates, and better discriminate among covariates which may affect these rate parameters.

Conclusions

Lentic Habitats

We recommend continuing to survey wetland habitats each year. In this preliminary study (2005-2007), the estimates of occupancy probabilities over time were relatively constant; however, the occupancy state did change among wetlands. In other words, some sites were colonized and others failed to support breeding and/or foraging activity (i.e., went locally extinct). An alternate year survey design cannot be used to estimate annual rates of change in any parameter of interest and the ability to detect temporal trends in occupancy and other rate parameters is sufficiently reduced in most scenarios (Table 9). At this point we do not know if extinction and colonization probabilities are constant over time or vary widely between years due to environmental conditions (i.e., rainfall, hydroperiod) or changes in

these conditions due to urbanization, and thus we caution against an alternate year survey design.

Lotic Habitats

We recommend continued surveying for lotic amphibians, to assess whether rate parameters are constant (or vary over time) and to elucidate the relationships between occupancy, rate parameters, and site-specific covariates (e.g., stream spatial configuration, proximity to the park boundary or internal park road, park, and transect location). We note that more sites (streams) are needed to reduce the uncertainty among models, and to improve estimates of the rate parameters. One major limitation in increasing the current number of streams monitored is obtaining accurate maps of small habitat features, including headwater streams and tributaries, for parks in the National Capital Region (NCR). Such a map is needed for expansion into areas such as Catoclin Mountain Park and one or more of the Historic parks in the NCR.

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Table 1. Latitude and longitude coordinates for wetlands surveyed in the Chesapeake and Ohio NHP (2005-2007).

Park	Site Name	Latitude	Longitude
C & O Canal NHP	Carderock Lot 3	38.9765	-77.2060
C & O Canal NHP	CHW05	38.9271	-77.1126
C & O Canal NHP	CHW06	38.9291	-77.1147
C & O Canal NHP	CHW09	38.9358	-77.1183
C & O Canal NHP	DC045	38.9139	-77.1003
C & O Canal NHP	GOBACK	38.9913	-77.2459
C & O Canal NHP	MD014	39.0191	-77.2383
C & O Canal NHP	MD014A	39.0182	-77.2391
C & O Canal NHP	MD025	39.0144	-77.2405
C & O Canal NHP	MD028	39.0134	-77.2417
C & O Canal NHP	MD039	39.0067	-77.2446
C & O Canal NHP	MD041	39.0062	-77.2450
C & O Canal NHP	MD042	39.0056	-77.2454
C & O Canal NHP	MD052	38.9933	-77.2456
C & O Canal NHP	MD053	38.9930	-77.2454
C & O Canal NHP	MD115	38.9833	-77.2414
C & O Canal NHP	MD118	38.9821	-77.2380
C & O Canal NHP	MD119B	38.9820	-77.2401
C & O Canal NHP	MD128	38.9843	-77.2392
C & O Canal NHP	MD129	38.9831	-77.2390
C & O Canal NHP	MD143	38.9834	-77.2370
C & O Canal NHP	MD144	38.9831	-77.2349
C & O Canal NHP	MD145	38.9832	-77.2355
C & O Canal NHP	MD146	38.9826	-77.2368
C & O Canal NHP	MD150	38.9817	-77.2349
C & O Canal NHP	MD155	38.9843	-77.2318
C & O Canal NHP	MD159	38.9812	-77.2261
C & O Canal NHP	MD204	38.9693	-77.1888
C & O Canal NHP	MD205	38.9694	-77.1879
C & O Canal NHP	MD211	38.9699	-77.1729
C & O Canal NHP	MD220	38.9628	-77.1371
C & O Canal NHP	MD240	38.9356	-77.1190
C & O Canal NHP	MD256X	38.9384	-77.1207

Table 2. Covariate definitions along with range, mean and standard deviation (SD) among 33 wetlands at the Chesapeake and Ohio NHP. Covariates were used to model initial occupancy probabilities and extinction and colonization probabilities for lentic amphibian species.

Covariate	Mean	+/-1SD	Range	Definition
Hydroperiod	4.0	1.2	1.7 to 5	Average hydroperiod score over 3 years. Score based on month of drying (1=April; 2=May;3=June; 4=July; 5=water present in July)
Area	0.05	0.05	0.001 to 0.247	Minimum wetland surface area(minimum length \times minimum width; hectares)
Flood Index	23	29	0 to 159	Slope($^{\circ}$) \times distance from river(m)
Cond	314	254	32 to 946	Maximum wetland conductivity(μ s)
Veg	0.27	0.45	0 or 1	Presence of Aquatic vegetation (1= \geq 15% aquatic vegetation present; 0= <15% aquatic vegetation)
Canopy	71	27	6 to 99	Maximum percent canopy cover

Table 3. The *a priori* expected relationship between the habitat covariates and the probability of occupancy. The species the relationship is expected for and the source for each of the predictions.

Covariate	Expected relationship with occupancy	Species relationship expected for	Source
Hydroperiod	+	All	Shoop 1974 Skelly et al. 1999 Babbitt et al. 2003
Wetland Area	+	All	Seale 1982 Armstrong 2005 Werner et al. 2007
Flood Index*	+	All	Dorcas et al. 2006
Conductivity	-	All	Glooschenko et al. 1992 Turtle 2000
Canopy Cover	-	<i>Bufo spp.</i> <i>P. crucifer</i> <i>R. clamitans</i>	Skelly et al. 1999
Aquatic Vegetation	+	<i>N. viridescens</i> <i>P. crucifer</i> <i>R. catesbeiana</i> <i>R. clamitans</i>	Egan and Paton 2004 Van Buskirk 2005 Kopp et al. 2006 Mazerolle et al. 2005

* For flood index lower values are more likely to flood.

Table 4. Occupancy structure of the candidate model set for wetland amphibians. See Table 2 for covariate definitions. The primary factors are the covariates we expected to have a strong influence on the probability of amphibian occupancy. Our candidate model set was designed to compare the relative importance of the variable within each set of factors (primary or secondary) and not between these sets.

Species	Primary Factors		Secondary Factors			
	Hydroperiod	Area	Flood	Cond	Veg	Canopy
<i>Ambystoma maculatum</i>	X		X			
	X			X		
		X	X			
		X		X		
	X	X	X			
	X	X		X		
	X					
		X				
	X	X				
			X			
				X		
<i>Bufo spp.</i>						X*
			X			X*
				X		X*
			X			
				X		
<i>Notophthalmus viridescens</i>	X		X			
	X			X		
	X				X	
		X	X			
		X		X		
		X			X	
	X	X	X			
	X	X		X		
	X	X			X	
	X					
		X				
	X	X				
			X			
				X		
					X	

* For *Bufo spp.* Canopy was considered the primary factor.

Table 4 *continued*. Candidate model set for wetland amphibians.

Species	Primary Factors		Secondary Factors			
	Hydroperiod	Area	Flood	Cond	Veg	Canopy
<i>Pseudacris crucifer</i>	X		X			
	X			X		
	X				X	
	X					X
		X	X			
		X		X		
		X			X	
		X				X
	X	X	X			
	X	X		X		
	X	X			X	
	X	X				X
	X					
		X				
	X	X				
			X			
				X		
					X	
						X
<i>Rana catesbeiana</i>	X		X			
	X			X		
	X				X	
		X	X			
		X		X		
		X			X	
	X	X	X			
	X	X		X		
	X	X			X	
	X					
		X				
	X	X				
			X			
				X		
					X	

Table 4 *continued*. Candidate model set for wetland amphibians.

Species	Primary Factors		Secondary Factors			
	Hydroperiod	Area	Flood	Cond	Veg	Canopy
<i>Rana clamitans</i>	X		X			
	X			X		
	X				X	
	X					X
		X	X			
		X		X		
		X			X	
		X				X
	X	X	X			
	X	X		X		
	X	X			X	
		X				X
	X					
		X				
	X	X				
			X			
				X		
					X	
						X
<i>Rana palustris</i>	X		X			
	X			X		
		X	X			
		X		X		
	X	X	X			
	X	X		X		
	X					
		X				
	X	X				
			X			
				X		
<i>Rana sylvatica</i>	X		X			
	X			X		
		X	X			
		X		X		
	X	X	X			
	X	X		X		
	X					
		X				
	X	X				
			X			
				X		

Table 5. Four scenarios describing possible change in occupancy probabilities over five years for selected amphibians (*Ambystoma maculatum* and *Notophthalmus viridescens*). Scenarios had either constant rate parameters (γ , ϵ) or they had a repeating cycle of one good year (γ_{good} , ϵ_{good}) followed by two bad years (γ_{bad} , ϵ_{bad}). Occupancy and rate parameter values were based on estimates from our analysis of 2005-2007 data. For *Ambystoma maculatum* we modeled two groups of wetland sites: Long Hydroperiod and Short Hydroperiod.

Notophthalmus viridescens

	$\gamma(\cdot)$	$\epsilon(\cdot)$	ψ_1	ψ_2	ψ_3	ψ_4	ψ_5
Scenario 1: 50% decline in occupancy assuming $\gamma(\cdot)$, and $\epsilon(\cdot)$							
	0.05	0.60	0.15	0.10	0.09	0.08	0.08

Ambystoma maculatum

	$\gamma(\cdot)$	γ_{good}	γ_{bad}	$\epsilon(\cdot)$	ϵ_{good}	ϵ_{bad}	ψ_1	ψ_2	ψ_3	ψ_4	ψ_5
Scenario 1: 50% decline in occupancy assuming $\gamma(\cdot)$, and $\epsilon(\cdot)$											
Long Hydroperiod	0.10			0.35			0.55	0.40	0.32	0.28	0.25
Short Hydroperiod	0.05			0.9			0.05	0.05	0.05	0.05	0.05
Overall							0.34	0.25	0.21	0.18	0.16
Scenario 2: 50% decline in occupancy assuming $\gamma_{\text{good}}, \epsilon_{\text{good}}$ and $\epsilon_{\text{bad}}, \gamma_{\text{bad}}$											
Long Hydroperiod		0.15	0.05		0.20	0.55	0.55	0.51	0.25	0.15	0.25
Short Hydroperiod		0.05	0.03		0.70	0.95	0.05	0.06	0.03	0.03	0.06
Overall							0.34	0.31	0.16	0.10	0.17
Scenario 3: 50% increase in occupancy assuming $\gamma(\cdot)$, and $\epsilon(\cdot)$											
Long Hydroperiod	0.4			0.1			0.55	0.68	0.74	0.77	0.78
Short Hydroperiod	0.1			0.7			0.05	0.11	0.12	0.12	0.13
Overall							0.34	0.43	0.47	0.49	0.50
Scenario 4: Detecting change in distribution assuming $\psi_1 = \psi_5$, $\gamma(t)$, $\epsilon(t)$											
Long Hydroperiod		0.25	0.05		0.1	0.3	0.55	0.61	0.44	0.34	0.47
Short Hydroperiod		0.10	0.05		0.05	0.85	0.05	0.14	0.06	0.06	0.15
Overall							0.34	0.41	0.28	0.22	0.33

Table 6. Summary of model selection statistics and beta coefficient estimates for variable in models with $\Delta AIC < 8$. Amphibian data was collected at Chesapeake and Ohio NHP wetlands from 2005-2007. ΔAIC is the difference in AIC value for a particular model when compared with the top ranked model; w is the AIC model weight; K is the number of parameters; $-2l$ is twice the negative log-likelihood value. Refer to Table 2 for explanations of the covariates. Hydroperiod is abbreviated as Hydro in this table. The detection covariates are defined as: $wtemp$ (water temperature/10($^{\circ}C$)), $wtemp^2$ ((water temperature/10) 2 ($^{\circ}C$)), and $visit+yr$ (visit with an additive year affect). Canopy, flood, hydro, and cond were standardized. We indicate when colonization or extinction estimates were fixed at zero in the following manner: $\gamma_2=0$ where colonization probability between years 2-3(2006-2007) equals zero.

Model	ΔAIC	w	K	$-2l$	Hydro	Area	Occupancy				Extinction	Colonization
							Flood	Cond	Veg	Canopy	Hydro	Area
<i>Ambystoma maculatum</i>												
$\psi(\text{Hydro,Area,Flood}),\gamma(\gamma_2=0),\varepsilon(\varepsilon_1=0),p(\text{visit}+yr)$	0.00	0.36	12	296.36	3.14	17.98	5.04					
$\psi(\text{Hydro,Flood}),\gamma(\gamma_2=0),\varepsilon(\varepsilon_1=0),p(\text{visit}+yr)$	0.45	0.29	11	298.81	3.02		3.95					
$\psi(\text{Hydro,Area,Flood}),\gamma(\text{Area},\gamma_2=0),\varepsilon(\varepsilon_1=0),p(\text{visit}+yr)$	1.37	0.18	13	295.73	3.14	17.98	5.04					
$\psi(\text{Hydro,Flood}),\gamma(\text{Area},\gamma_2=0),\varepsilon(\varepsilon_1=0),p(\text{visit}+yr)$	1.82	0.15	12	298.18	3.02		3.95					-8.99
Model Average Estimate					3.08	17.98	4.56					-8.99
Unconditional SE					1.52	11.78	1.80					13.08
<i>Bufo spp.</i>												
$\psi(.),\gamma(.),\varepsilon(.),p(wtemp^2)$	0.00	0.37	6	331.14								
$\psi(\text{Flood}),\gamma(.),\varepsilon(.),p(wtemp^2)$	1.51	0.17	7	330.65			0.28					
$\psi(\text{Canopy}),\gamma(.),\varepsilon(.),p(wtemp^2)$	1.57	0.17	7	330.71						0.25		
$\psi(\text{Cond}),\gamma(.),\varepsilon(.),p(wtemp^2)$	1.79	0.15	7	330.93				-0.21				
$\psi(\text{Canopy,Flood}),\gamma(.),\varepsilon(.),p(wtemp^2)$	3.33	0.07	8	330.47			0.21			0.17		
$\psi(\text{Canopy,Cond}),\gamma(.),\varepsilon(.),p(wtemp^2)$	3.53	0.06	8	330.67				-0.10		0.21		
Model Average Estimate							0.26	-0.18		0.22		
Unconditional SE							0.44	0.47		0.39		

Table 6 *continued*. Summary of model selection statistics for models ($\Delta AIC < 8$) for amphibian data collected at Chesapeake and Ohio NHP wetlands from 2005-2007.

Model	ΔAIC	w	K	-2l	Hydro	Area	Occupancy			Extinction	Colonization	
							Flood	Cond	Veg	Canopy	Hydro	Area
<i>Notophthalmus viridescens</i>												
ψ(Veg),γ(.),ε(.),p(.)	0.00	0.49	5	184.00					2.88			
ψ(Area, Veg),γ(.),ε(.),p(.)	1.42	0.24	6	183.42		7.91			2.89			
ψ(Hydro,Area,Cond),γ(.),ε(.),p(.)	2.33	0.15	7	182.33	81.82	-1.01		-0.70				
ψ,γ(.),ε(.),p(.)	5.18	0.04	4	191.18								
ψ(Cond),γ(.),ε(.),p(.)	5.77	0.03	5	189.77				-0.79				
ψ(Area),γ(.),ε(.),p(.)	6.44	0.02	5	190.44		7.10						
ψ(Flood),γ(.),ε(.),p(.)	6.78	0.02	5	190.78			0.26					
ψ(Area, Cond),γ(.),ε(.),p(.)	6.98	0.01	6	188.98		8.28		-0.85				
ψ(Area,Flood),γ(.),ε(.),p(.)	7.75	0.01	6	189.75		8.82	0.36					
Model Average Estimate					81.82	4.80	0.30	-0.73	2.88			
Unconditional SE					2.49	10.82	0.41	0.80	1.23			
<i>Pseudacris crucifer</i>												
ψ(Hydro,Canopy),γ(.),ε(.),p(visit+yr)	0.00	0.42	11	189.94	3.44					3.83		
ψ(Hydro,Area,Canopy),γ(.),ε(.),p(visit+yr)	1.50	0.20	12	189.44	3.35	7.57				4.39		
ψ(Hydro,Canopy),γ(.),ε(Hydro),p(visit+yr	1.98	0.16	12	189.92	3.44					3.83	-0.43	
ψ(Hydro,Area,Canopy),γ(.),ε(Hydro),p(visit+yr)	3.48	0.07	13	189.42	3.35	7.57				4.39	-0.43	
ψ(Area,Canopy),γ(.),ε(.),p(visit+yr)	5.52	0.03	11	195.46		14.21				4.06		
ψ(Canopy),γ(.),ε(.),p(visit+yr)	5.67	0.02	10	197.61						3.04		
ψ(Hydro,Cond),γ(.),ε(.),p(visit+yr)	6.76	0.01	11	196.70	2.17			-2.11				
ψ(Area,Canopy),γ(.),ε(Hydro),p(visit+yr)	7.48	0.01	12	195.42		14.19				4.05	-0.46	
ψ(Canopy),γ(.),ε(Hydro),p(visit+yr)	7.63	0.01	11	197.57						3.04	-0.47	
Model Average Estimate					3.39	8.35		-2.11		3.97	-0.43	
Unconditional SE					1.95	11.02		1.21		2.05	2.65	

Table 6 *continued*. Summary of model selection statistics for models ($\Delta AIC < 8$) for amphibian data collected at Chesapeake and Ohio NHP wetlands from 2005-2007.

Model	ΔAIC	w	K	-2l	Hydro	Area	Occupancy			Canopy	Extinction	Colonization
							Flood	Cond	Veg		Hydro	Area
<i>Rana catesbeiana</i>												
ψ(Hydro,Veg),γ(.),ε(ε2=0),p(wtemp²)	0.00	0.29	8	343.99	2.45					-2.42		
ψ(Hydro,Veg),γ(.),ε(Hydro,ε2=0),p(wtemp²)	1.05	0.17	9	343.04	2.37					-2.37	-4.10	
ψ(Hydro,Area,Veg),γ(.),ε(ε2=0),p(wtemp²)	2.00	0.11	9	343.99	2.47	-0.40				-2.43		
ψ(Hydro),γ(.),ε(ε2=0),p(wtemp²)	2.54	0.08	7	348.53	1.61							
ψ(Hydro,Area,Veg) γ(.),ε(Hydro,ε2=0),p(wtemp²)	3.05	0.06	10	343.04	2.36	0.20				-2.36	-4.11	
ψ(Hydro),γ(.),ε(Hydro,ε2=0),p(wtemp²)	3.49	0.05	8	347.48	1.56						-5.58	
ψ(Hydro,Flood),γ(.),ε(ε2=0),p(wtemp²)	3.64	0.05	8	347.63	1.57		-0.42					
ψ(Hydro,Area),γ(.),ε(ε2=0),p(wtemp²)	4.44	0.03	8	348.43	1.49	3.03						
ψ(Hydro,Cond),γ(.),ε(ε2=0),p(wtemp²)	4.54	0.03	8	348.53	1.61			0.00				
ψ(Hydro,Cond), γ(.),ε(Hydro,ε2=0),p(wtemp²)	5.49	0.02	9	347.48	1.55			-0.02			-5.58	
ψ(Hydro,Area,Flood),γ(.),ε(ε2=0),p(wtemp²)	5.63	0.02	9	347.62	1.54	0.91	-0.41					
ψ(Hydro,Area,Cond) γ(.),ε(ε2=0),p(wtemp²)	6.44	0.01	9	348.43	1.48	3.07		-0.02				
ψ(Area),γ(.),ε(ε2=0),p(wtemp²)	6.57	0.01	7	352.56		12.47						
ψ(Area),γ(.),ε(Hydro,ε2=0),p(wtemp²)	6.74	0.01	8	350.73		13.80					-383.84	
ψ(Flood),γ(.),ε(ε2=0),p(wtemp²)	7.47	0.01	7	353.46			-0.51					
ψ(Area,Veg),γ(.),ε(ε2=0),p(wtemp²)	7.56	0.01	8	351.55		13.49			-0.96			
ψ(Veg),γ(.),ε(ε2=0),p(wtemp²)	7.82	0.01	7	353.81					-0.85			
ψ(Area,Flood) γ(.),ε(ε2=0),p(wtemp²)	7.94	0.01	8	351.93		11.06	-0.36					
ψ(Veg),γ(.),ε(Hydro,ε2=0),p(wtemp²)	7.97	0.01	8	351.96					-0.93		-5.17	
Model Average Estimate					2.15	1.59	-0.42	-0.01	-2.36		-4.45	
Unconditional SE					1.07	11.02	0.51	0.58	1.30		9.59	

Table 6 *continued*. Summary of model selection statistics for models ($\Delta AIC < 8$) for amphibian data collected at Chesapeake and Ohio NHP wetlands from 2005-2007.

Model	ΔAIC	w	K	$-2l$	Hydro	Area	Occupancy			Canopy	Extinction	Colonization
							Flood	Cond	Veg		Hydro	Area
<i>Rana clamitans</i>												
$\psi(\text{Hydro,Canopy}),\gamma(.),\varepsilon(\text{Hydro}),p(\text{wtemp}^2)$	0.00	0.78	9	472.24	7.01					3.79	-2.48	
$\psi(\text{Hydro,Canopy}),\gamma(.),\varepsilon(.),p(\text{wtemp}^2)$	2.61	0.21	8	476.85	7.01					3.79		
Model Average Estimate					7.01					3.79	-2.48	
Unconditional SE					3.39					1.82	1.27	
<i>Rana palustris</i>												
$\psi(\text{Hydro,Area,Flood}),\gamma(.),\varepsilon(.),p(\text{wtemp}^2)$	0.00	1.00	9	274	187.49	-0.97	4.25					

Table 6 *continued*. Summary of model selection statistics for models ($\Delta AIC < 8$) for amphibian data collected at Chesapeake and Ohio NHP wetlands from 2005-2007.

Model	ΔAIC	w	K	-2l	Hydro	Area	Occupancy				Extinction	Colonization
							Flood	Cond	Veg	Canopy	Hydro	Area
<i>Rana sylvatica</i>												
ψ(Hydro,Area,Flood),γ(.),ε(.),p(visit+yr)	0.00	0.28	12	354.91	1.59	34.28	2.90					
ψ(Hydro,Area,Cond),γ(.),ε(.),p(visit+yr)	1.48	0.13	12	356.39	0.98	19.33		-1.83				
ψ(Area,Cond),γ(.),ε(.),p(visit+yr)	1.86	0.11	11	358.77		26.68		-1.98				
ψ(Hydro,Area,Flood),γ(.),ε(Hydro),p(visit+yr)	1.93	0.11	13	354.84	1.57	33.87	2.86				-0.44	
ψ(Area,Flood),γ(.),ε(.),p(visit+yr)	2.46	0.08	11	359.37		36.48	1.65					
ψ(Hydro,Cond),γ(.),ε(.),p(visit+yr)	3.37	0.05	11	360.28	1.44			-1.40				
ψ(Hydro,Area,Cond),γ(.),ε(Hydro),p(visit+yr)	3.39	0.05	13	356.30	0.97	19.31		-1.83			-0.49	
ψ(Area,Cond),γ(.),ε(Hydro),p(visit+yr)	3.72	0.04	12	358.63		26.53		-1.98			-0.59	
ψ(Area,Flood),γ(.),ε(Hydro),p(visit+yr)	4.30	0.03	12	359.21		36.42	1.66				-0.60	
ψ(Hydro,Flood),γ(.),ε(.),p(visit+yr)	4.49	0.03	11	361.40	1.76		1.50					
ψ(Hydro,Cond),γ(.),ε(Hydro),p(visit+yr)	5.27	0.02	12	360.18	1.43			-1.40			-0.50	
ψ(Hydro,Area),γ(.),ε(.),p(visit+yr)	5.92	0.01	11	362.83	0.94	17.64						
ψ(Hydro,Flood),γ(.),ε(Hydro),p(visit+yr)	6.39	0.01	12	361.30	1.75		1.50				-0.49	
ψ(Area),γ(.),ε(.),p(visit+yr)	6.84	0.01	10	365.75		25.77						
ψ(Hydro),γ(.),ε(.),p(visit+yr)	7.07	0.01	10	365.98	1.39							
ψ(Hydro,Area),γ(.),ε(Hydro),p(visit+yr)	7.82	0.01	12	362.73	0.94	17.63					-0.50	
Model Average Estimate					1.40	29.51	2.52	-1.81			-0.50	
Unconditional SE					1.00	19.75	2.03	0.96			1.41	

Table 7. Initial occupancy ψ and extinction ε and colonization γ structures for the candidate model set fit to data from each of 3 salamander species, using multi-season occupancy models. Covariates include: ‘transloc’, a categorical variable indicating whether a transect pair is located near the headwaters (= 0) or 145 m from the stream origin (= 1); ‘park’, a categorical variable indicating whether a stream was found in ROCR (= 1) vs. CHOH (= 0); ‘network’, a categorical variable indicating whether a stream has a confluent, first order branch (i.e., a branched stream; = 1) or not (i.e., an unbranched stream; = 0); ‘nrbound’, a categorical indicator, whether the stream begins within 100 m of the park boundary or a major internal park road (= 1 if true, 0 otherwise). The notation (.) specifies a constant probability, while a (0) specifies no extinction or colonization.

Model	ψ	γ	ε	Model name
1	park	0	0	$\psi(\text{park}) \gamma(0) \varepsilon(0)$
2	park	0	nrbound	$\psi(\text{park}) \gamma(0) \varepsilon(\text{nrbound})$
3	park	.	.	$\psi(\text{park}) \gamma(.) \varepsilon(.)$
4	park	.	nrbound	$\psi(\text{park}) \gamma(.) \varepsilon(\text{nrbound})$
5	park	network	0	$\psi(\text{park}) \gamma(\text{network}) \varepsilon(0)$
6	park	network	.	$\psi(\text{park}) \gamma(\text{network}) \varepsilon(.)$
7	park	network	nrbound	$\psi(\text{park}) \gamma(\text{network}) \varepsilon(\text{nrbound})$
8	park	network	year	$\psi(\text{park}) \gamma(\text{network}) \varepsilon(\text{year})$
9	park	year	nrbound	$\psi(\text{park}) \gamma(\text{year}) \varepsilon(\text{nrbound})$
10	park	year	year	$\psi(\text{park}) \gamma(\text{year}) \varepsilon(\text{year})$
11	park, nrbound	0	0	$\psi(\text{park, nrbound}) \gamma(0) \varepsilon(0)$
12	park, nrbound	0	nrbound	$\psi(\text{park, nrbound}) \gamma(0) \varepsilon(\text{nrbound})$
13	park, nrbound	.	.	$\psi(\text{park, nrbound}) \gamma(.) \varepsilon(.)$
14	park, nrbound	.	nrbound	$\psi(\text{park, nrbound}) \gamma(.) \varepsilon(\text{nrbound})$
15	park, nrbound	network	0	$\psi(\text{park, nrbound}) \gamma(\text{network}) \varepsilon(0)$
16	park, nrbound	network	.	$\psi(\text{park, nrbound}) \gamma(\text{network}) \varepsilon(.)$
17	park, nrbound	network	nrbound	$\psi(\text{park, nrbound}) \gamma(\text{network}) \varepsilon(\text{nrbound})$
18	park, nrbound	network	year	$\psi(\text{park, nrbound}) \gamma(\text{network}) \varepsilon(\text{year})$
19	park, nrbound	year	nrbound	$\psi(\text{park, nrbound}) \gamma(\text{year}) \varepsilon(\text{nrbound})$
20	park, nrbound	year	year	$\psi(\text{park, nrbound}) \gamma(\text{year}) \varepsilon(\text{year})$
21	park, transloc	0	0	$\psi(\text{park, transloc}) \gamma(0) \varepsilon(0)$
22	park, transloc	0	nrbound	$\psi(\text{park, transloc}) \gamma(0) \varepsilon(\text{nrbound})$
23	park, transloc	.	.	$\psi(\text{park, transloc}) \gamma(.) \varepsilon(.)$
24	park, transloc	.	nrbound	$\psi(\text{park, transloc}) \gamma(.) \varepsilon(\text{nrbound})$
25	park, transloc	network	0	$\psi(\text{park, transloc}) \gamma(\text{network}) \varepsilon(0)$
26	park, transloc	network	.	$\psi(\text{park, transloc}) \gamma(\text{network}) \varepsilon(.)$
27	park, transloc	network	nrbound	$\psi(\text{park, transloc}) \gamma(\text{network}) \varepsilon(\text{nrbound})$
28	park, transloc	network	year	$\psi(\text{park, transloc}) \gamma(\text{network}) \varepsilon(\text{year})$
29	park, transloc	year	nrbound	$\psi(\text{park, transloc}) \gamma(\text{year}) \varepsilon(\text{nrbound})$
30	park, transloc	year	year	$\psi(\text{park, transloc}) \gamma(\text{year}) \varepsilon(\text{year})$
31	transloc	0	0	$\psi(\text{transloc}) \gamma(0) \varepsilon(0)$

Table 7 *continued*. Initial occupancy ψ and extinction ε and colonization γ structures for the candidate model set fit to data from each of 3 salamander species.

Model	ψ	γ	ε	Model name
32	transloc	0	nrbound	$\psi(\text{transloc}) \gamma(0) \varepsilon(\text{nrbound})$
33	transloc	.	.	$\psi(\text{transloc}) \gamma(.) \varepsilon(.)$
34	transloc	.	nrbound	$\psi(\text{transloc}) \gamma(.) \varepsilon(\text{nrbound})$
35	transloc	network	0	$\psi(\text{transloc}) \gamma(\text{network}) \varepsilon(0)$
36	transloc	network	.	$\psi(\text{transloc}) \gamma(\text{network}) \varepsilon(.)$
37	transloc	network	nrbound	$\psi(\text{transloc}) \gamma(\text{network}) \varepsilon(\text{nrbound})$
38	transloc	network	year	$\psi(\text{transloc}) \gamma(\text{network}) \varepsilon(\text{year})$
39	transloc	year	bound	$\psi(\text{transloc}) \gamma(\text{year}) \varepsilon(\text{bound})$
40	transloc	year	year	$\psi(\text{transloc}) \gamma(\text{year}) \varepsilon(\text{year})$
41	transloc, nrbound	0	0	$\psi(\text{transloc, nrbound}) \gamma(0) \varepsilon(0)$
42	transloc, nrbound	0	nrbound	$\psi(\text{transloc, nrbound}) \gamma(0) \varepsilon(\text{nrbound})$
43	transloc, nrbound	.	.	$\psi(\text{transloc, nrbound}) \gamma(.) \varepsilon(.)$
44	transloc, nrbound	.	nrbound	$\psi(\text{transloc, nrbound}) \gamma(.) \varepsilon(\text{nrbound})$
45	transloc, nrbound	network	0	$\psi(\text{transloc, nrbound}) \gamma(\text{network}) \varepsilon(0)$
46	transloc, nrbound	network	.	$\psi(\text{transloc, nrbound}) \gamma(\text{network}) \varepsilon(.)$
47	transloc, nrbound	network	nrbound	$\psi(\text{transloc, nrbound}) \gamma(\text{network}) \varepsilon(\text{nrbound})$
48	transloc, nrbound	network	year	$\psi(\text{transloc, nrbound}) \gamma(\text{network}) \varepsilon(\text{year})$
49	transloc, nrbound	year	nrbound	$\psi(\text{transloc, nrbound}) \gamma(\text{year}) \varepsilon(\text{nrbound})$
50	transloc, nrbound	year	year	$\psi(\text{transloc, nrbound}) \gamma(\text{year}) \varepsilon(\text{year})$

Table 8. Estimates of year-specific occupancy probabilities, extinction and colonization probabilities for the eight amphibian species found in the Chesapeake and Ohio NHP. These estimates are based on a model with constant occupancy, colonization, extinction probabilities ($\psi(\cdot)$, $\gamma(\cdot)$, $\epsilon(\cdot)$) and the probability of detection modeled as varying by visit or varying by visit with an additive year affect. ψ_{2006} and ψ_{2007} are derived estimates

Species	ψ_{2005} (SE)	ψ_{2006} (SE)	ψ_{2007} (SE)	ϵ (SE)	γ (SE)
<i>Ambystoma maculatum</i>	0.27 (0.08)	0.33 (0.08)	0.37 (0.09)	0.05 (0.05)	0.09 (0.04)
<i>Bufo spp.</i>	0.53 (0.10)	0.57 (0.10)	0.59 (0.12)	0.08 (0.09)	0.18 (0.10)
<i>Notophthalmus viridescens</i>	0.15 (0.06)	0.14 (0.06)	0.13 (0.06)	0.22 (0.14)	0.02 (0.02)
<i>Pseudacris crucifer</i>	0.25 (0.08)	0.27 (0.08)	0.28 (0.09)	0.51 (0.15)	0.20 (0.09)
<i>Rana catesbeiana</i>	0.53 (0.11)	0.60 (0.09)	0.62 (0.12)	0.18 (0.09)	0.33 (0.14)
<i>Rana clamitans</i>	0.68 (0.09)	0.53 (0.08)	0.43 (0.10)	0.27 (0.08)	0.10 (0.09)
<i>Rana palustris</i>	0.40 (0.17)	0.31 (0.10)	0.24 (0.08)	0.23 (0.10)	<0.01 (0.10)
<i>Rana sylvatica</i>	0.37 (0.08)	0.34 (0.07)	0.32 (0.08)	0.18 (0.09)	0.06 (0.04)

Table 9. Approximation of power to detect occupancy changes for 4 simulated scenarios (see Table 5 for details). Four long-term sampling designs are explored for each scenario including: surveying 35 sites annually, surveying 35 sites every 2 years, surveying 70 sites annually, or surveying 70 sites every 2 years. Power is approximated using a likelihood ratio test the null hypothesis (H_0 : constant occupancy probabilities, signifying no change) vs. the alternative hypothesis (H_a : year-specific occupancy or occupancy status changes over time). The resulting chi-square statistic (χ^2) is used as the noncentrality parameter and power is calculated from a non-central chi-squared distribution (see Burnham et al. 1987). $\psi(\cdot)$, $\gamma(\cdot)$, and $\epsilon(\cdot)$ represent time-constant occupancy, colonization and extinction probabilities respectively. $\psi(t)$, $\gamma(t)$, and $\epsilon(t)$ represent time-specific occupancy, colonization and extinction probabilities respectively. γ_{good} , γ_{bad} and ϵ_{good} , ϵ_{bad} represent colonization and extinction probabilities that vary between good and bad years.

Notophthalmus viridescens

Sampling Frequency	Number of Sites	χ^2	df	power(α 0.05)	power(α 0.10)
<i>Scenario 1: 50% decline in occupancy assuming $\gamma(\cdot)$, $\epsilon(\cdot)$</i>					
H_0 : $\psi(\cdot)$ H_a : $\psi(t)$					
Every year	35	1.3	3	14%	22%
Alternating year	35	1.2	3	13%	21%
Every year	70	2.6	3	24%	35%
Alternating year	70	2.4	3	22%	33%

Ambystoma maculatum

Sampling Frequency	Number of Sites	χ^2	df	power(α 0.05)	power(α 0.10)
<i>Scenario 1: 50% decline in occupancy assuming $\gamma(t)$, $\epsilon(t)$</i>					
H_0 : $\psi(\cdot)$ H_a : $\psi(t)$					
Every year	35	5.1	6	34%	47%
Alternating year	35	4.7	6	32%	44%
Every year	70	10.0	6	64%	76%
Alternating year	70	9.5	6	62%	73%
<i>Scenario 2: 50% decline in occupancy assuming $\gamma_{\text{good}}, \epsilon_{\text{good}}$ and $\epsilon_{\text{bad}}, \gamma_{\text{bad}}$</i>					
H_0 : $\psi(\cdot)$ and $\epsilon(\cdot)$ vs. H_a : $\psi(t)$, $\epsilon(t)$					
Every year	35	11.5	6	72%	81%
Alternating year	35	6.2	6	42%	55%
Every year	70	23.0	6	97%	99%
Alternating year	70	12.4	6	76%	84%

Table 9 *continued*. Approximation of power to detect occupancy change under four simulated scenarios (see Table 5 for details).

Ambystoma maculatum

Sampling Frequency	Number of Sites	χ^2	df	power(α 0.05)	power(α 0.10)
<i>Scenario 3: 50% increase in occupancy assuming $\gamma(\cdot)$, $\varepsilon(\cdot)$</i>					
<i>$H_0: \psi(\cdot)$ vs. $H_a: \psi(t)$</i>					
Every year	35	4.1	6	28%	39%
Every year	70	8.2	6	54%	66%
<i>Scenario 4: Detecting change in distribution $\psi_1 = \psi_5$, $\gamma(t)$, $\varepsilon(t)$</i>					
<i>$H_0: \psi(\cdot)$ and $\varepsilon(\cdot)$ vs. $H_a: \psi(\cdot), \varepsilon(t)$</i>					
Every year	35	7.8	6	52%	64%
Alternating year	35	1.4	6	11%	19%
Every year	70	15.5	6	86%	92%
Alternating year	70	2.7	6	19%	29%

Table 10. Summary of model selection statistics for all candidate models fit to steam (lotic) salamander data at Chesapeake and Ohio NHP and Rock Creek Park from 2005-2007. ΔAIC is the difference in AIC value for a particular model when compared with the top ranked model; w is the AIC model weight; K is the number of parameters; $-2l$ is twice the negative log-likelihood value. Refer to Table 7 for explanations of the covariates. (.) specifies a constant probability, while (0) specifies rate parameter probabilities that are constrained to be zero(i.e., no extinction or colonization between years). ‘Month’ allows a different detection probability (p) between June and July, while ‘year’ refers to probabilities that differ between 2005-06 and 2006-07. Models for each species above the thin line were used in model averaging (sum of Akaike weights ≥ 0.95); models listed below the bold line(in red font) did not converge and were not used to calculate model weights. Models in italics were either used to investigate covariate structures on detection probability or investigated *a posteriori*; these models were not used to calculate model weights for model averaging.

<i>Desmognathus fuscus</i>					
Model	AIC	ΔAIC	w	K	$-2l$
$\psi(\text{transloc}, \text{park}), \gamma(.), \varepsilon(.), p(\text{month})$	247.03	0.00	0.167	7	233.03
$\psi(\text{transloc}, \text{park}), \gamma(\text{network}), \varepsilon(.), p(\text{month})$	248.07	1.04	0.099	8	232.07
$\psi(\text{transloc}, \text{park}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{month})$	248.31	1.28	0.088	9	230.31
$\psi(\text{park}), \gamma(.), \varepsilon(.), p(\text{month})$	248.77	1.74	0.070	6	236.77
$\psi(\text{park}, \text{transloc}), \gamma(\text{network}), \varepsilon(0), p(\text{month})$	248.91	1.87	0.065	7	234.91
$\psi(\text{transloc}, \text{park}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{month})$	249.03	2.00	0.061	8	233.03
<i>$\psi(\text{transloc}, \text{park}), \gamma(.), \varepsilon(.), p(\text{month}, \text{year})$</i>	249.58	2.55	0.047	9	231.58
$\psi(\text{transloc}, \text{park}), \gamma(\text{year}), \varepsilon(\text{nrbound}), p(\text{month})$	249.76	2.73	0.043	9	231.76
<i>$\psi(\text{transloc}, \text{park}), \gamma(\text{network} + \text{park}), \varepsilon(.), p(\text{month})$</i>	249.83	2.79	0.041	9	231.83
$\psi(\text{nrbound}, \text{park}), \gamma(.), \varepsilon(.), p(\text{month})$	249.97	2.94	0.038	7	235.97
$\psi(\text{park}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{month})$	250.58	3.54	0.028	8	234.58
$\psi(\text{park}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{month})$	250.77	3.74	0.026	7	236.77
$\psi(\text{nrbound}, \text{park}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{month})$	250.98	3.95	0.023	9	232.98
$\psi(\text{park}), \gamma(\text{network}), \varepsilon(0), p(\text{month})$	251.12	4.08	0.022	6	239.12
$\psi(\text{nrbound}, \text{park}), \gamma(\text{network}), \varepsilon(.), p(\text{month})$	251.51	4.48	0.018	8	235.51
$\psi(\text{park}), \gamma(\text{year}), \varepsilon(\text{nrbound}), p(\text{month})$	251.60	4.57	0.017	8	235.60
$\psi(\text{nrbound}, \text{park}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{month})$	251.72	4.69	0.016	9	233.72
$\psi(\text{transloc}), \gamma(.), \varepsilon(.), p(\text{month})$	251.94	4.91	0.014	6	239.94
<i>$\psi(\text{nrbound}, \text{park}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{month})$</i>	251.97	4.94	0.014	8	235.97
$\psi(\text{nrbound}, \text{park}), \gamma(\text{network}), \varepsilon(0), p(\text{month})$	252.24	5.21	0.012	7	238.24
$\psi(\text{park}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{month})$	252.37	5.33	0.012	8	236.37
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{month})$	252.66	5.63	0.010	8	236.66
<i>$\psi(\text{nrbound}, \text{park}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{year})$</i>	252.74	5.71	0.010	9	234.74
$\psi(\text{nrbound}, \text{park}), \gamma(\text{year}), \varepsilon(\text{nrbound}), p(\text{month})$	252.80	5.77	0.009	9	234.80
$\psi(\text{nrbound}, \text{park}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{month})$	253.51	6.48	0.007	9	235.51
$\psi(\text{transloc}, \text{nrbound}), \gamma(.), \varepsilon(.), p(\text{month})$	253.87	6.83	0.005	7	239.87
$\psi(\text{transloc}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{month})$	253.94	6.91	0.005	7	239.94

$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{network}), \varepsilon(.), p(\text{month})$	254.26	7.23	0.004	8	238.26
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{month})$	254.40	7.37	0.004	8	238.40
$\psi(\text{transloc}), \gamma(\text{year}), \varepsilon(\text{nrbound}), p(\text{month})$	254.49	7.46	0.004	8	238.49
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{month})$	254.53	7.50	0.004	9	236.53
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{month})$	254.64	7.61	0.004	9	236.64
$\psi(\text{nrbound}, \text{park}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{month}, \text{year})$	254.65	7.61	0.004	10	234.65
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{network}), \varepsilon(0), p(\text{month})$	255.10	8.06	0.003	7	241.10
$\psi(\text{transloc}, \text{nrbound}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{month})$	255.86	8.83	0.002	8	239.86
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{month})$	256.26	9.23	0.002	9	238.26
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{year}), \varepsilon(\text{nrbound}), p(\text{month})$	256.41	9.37	0.002	9	238.41
$\psi(\text{park}), \gamma(0), \varepsilon(0), p(\text{month})$	276.00	28.97	0.000	4	268.00
$\psi(\text{nrbound}, \text{park}), \gamma(0), \varepsilon(0), p(\text{month})$	276.87	29.84	0.000	5	266.87
$\psi(\text{transloc}, \text{park}), \gamma(0), \varepsilon(0), p(\text{month})$	277.39	30.36	0.000	5	267.39
$\psi(\text{transloc}), \gamma(0), \varepsilon(0), p(\text{month})$	277.43	30.40	0.000	4	269.43
$\psi(\text{transloc}, \text{nrbound}), \gamma(0), \varepsilon(0), p(\text{month})$	279.08	32.05	0.000	5	269.08
$\psi(\text{park}), \gamma(0), \varepsilon(\text{nrbound}), p(\text{month})$	279.44	32.41	0.000	6	267.44
$\psi(\text{nrbound}, \text{park}), \gamma(0), \varepsilon(\text{nrbound}), p(\text{month})$	280.31	33.28	0.000	7	266.31
$\psi(\text{transloc}, \text{park}), \gamma(0), \varepsilon(\text{nrbound}), p(\text{month})$	280.83	33.80	0.000	7	266.83
$\psi(\text{transloc}), \gamma(0), \varepsilon(\text{nrbound}), p(\text{month})$	280.87	33.84	0.000	6	268.87
$\psi(\text{transloc}, \text{nrbound}), \gamma(0), \varepsilon(\text{nrbound}), p(\text{month})$	282.52	35.49	0.000	7	268.52
$\psi(\text{transloc}, \text{nrbound}), \gamma(0), \varepsilon(.), p(\text{month})$	312.17	65.14	0.000	5	302.17
$\psi(\text{transloc}, \text{park}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{month})$	247.96			9	229.96
$\psi(\text{transloc}, \text{park}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{month})$	250.07			9	232.07
$\psi(\text{transloc}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{month})$	252.72			8	236.72
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(.), p(\text{month})$	252.40			7	238.40
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(0), p(\text{month})$	253.24			6	241.24
$\psi(\text{park}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{month})$	249.78			8	233.78
$\psi(\text{park}), \gamma(\text{network}), \varepsilon(.), p(\text{month})$	250.37			7	236.37

Pseudotriton ruber

Model	AIC	Δ AIC	w	K	-2l
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(0), p(\text{year})$	185.28	0.00	0.161	7	171.28
$\psi(\text{transloc}), \gamma(\text{park}+\text{network}), \varepsilon(0), p(\text{year})$	185.53	0.24	0.143	8	169.53
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{network}), \varepsilon(0), p(\text{year})$	185.71	0.42	0.130	8	169.71
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(0), p(\text{year}, \text{month})$	187.23	1.95	0.061	8	171.23
$\psi(\text{transloc}, \text{park}), \gamma(\text{network}), \varepsilon(0), p(\text{year})$	187.27	1.98	0.060	8	171.27
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(\cdot), p(\text{year})$	187.28	2.00	0.059	8	171.28
$\psi(\text{transloc}), \gamma(\text{park}, \text{network}), \varepsilon(\cdot), p(\text{year})$	187.53	2.24	0.053	9	169.53
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{network}), \varepsilon(\cdot), p(\text{year})$	187.71	2.42	0.048	9	169.71
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{year})$	188.13	2.85	0.039	9	170.13
$\psi(\text{transloc}, \text{nrbound}), \gamma(\cdot), \varepsilon(\cdot), p(\text{year})$	189.12	3.83	0.024	8	173.12
$\psi(\text{transloc}), \gamma(\cdot), \varepsilon(\cdot), p(\text{year})$	189.22	3.94	0.022	7	175.22
$\psi(\text{transloc}, \text{park}), \gamma(\text{network}), \varepsilon(\cdot), p(\text{year})$	189.27	3.98	0.022	9	171.27
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{year})$	189.28	4.00	0.022	9	171.28
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{year})$	189.71	4.42	0.018	10	169.71
$\psi(\text{transloc}), \gamma(\cdot), \varepsilon(\text{nrbound}), p(\text{year})^{**}$	189.87	4.58	0.016	8	173.87
$\psi(\text{transloc}, \text{park}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{year})$	190.12	4.84	0.014	10	170.12
$\psi(\text{transloc}, \text{nrbound}), \gamma(\cdot), \varepsilon(\text{nrbound}), p(\text{year})$	190.15	4.87	0.014	9	172.15
$\psi(\text{transloc}, \text{nrbound}, \text{network}), \gamma(\cdot), \varepsilon(\text{nrbound}), p(\text{year})$	190.27	4.99	0.013	10	170.27
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(0), p(\text{month})$	190.97	5.69	0.009	6	178.97
$\psi(\text{transloc}, \text{park}, \text{nrbound}), \gamma(\cdot), \varepsilon(\cdot), p(\text{year})$	191.06	5.78	0.009	9	173.06
$\psi(\text{transloc}, \text{park}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{year})$	191.27	5.98	0.008	10	171.27
$\psi(\text{transloc}, \text{park}), \gamma(\cdot), \varepsilon(\cdot), p(\text{year})$	191.11	5.83	0.009	8	175.11
$\psi(\text{transloc}, \text{park}), \gamma(\cdot), \varepsilon(\text{nrbound}), p(\text{year})$	191.76	6.48	0.006	9	173.76
$\psi(\text{transloc}, \text{nrbound}, \text{network}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{year}, \text{month})$	192.02	6.73	0.006	12	168.02
$\psi(\text{transloc}, \text{park}, \text{nrbound}), \gamma(\cdot), \varepsilon(\text{nrbound}), p(\text{year})$	192.11	6.83	0.005	10	172.11
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{year}), \varepsilon(\text{nrbound}), p(\text{year})$	192.14	6.86	0.005	10	172.14
$\psi(\text{transloc}, \text{nrbound}, \text{network}), \gamma(\cdot), \varepsilon(\text{nrbound}), p(\text{year}, \text{month})$	192.24	6.96	0.005	11	170.24
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{year})$	193.09	7.81	0.003	10	173.09
$\psi(\text{transloc}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{year})$	193.22	7.94	0.003	9	175.22
$\psi(\text{transloc}, \text{park}), \gamma(\text{year}), \varepsilon(\text{nrbound}), p(\text{year})$	193.76	8.48	0.002	10	173.76
$\psi(\text{transloc}, \text{nrbound}, \text{network}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{month})$	194.53	9.25	0.002	10	174.53
$\psi(\text{transloc}, \text{nrbound}), \gamma(0), \varepsilon(0), p(\text{year})$	194.71	9.43	0.001	6	182.71
$\psi(\text{transloc}, \text{nrbound}, \text{network}), \gamma(\cdot), \varepsilon(\text{nrbound}), p(\text{month})$	194.86	9.57	0.001	9	176.86
$\psi(\text{transloc}, \text{park}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{year})$	195.11	9.82	0.001	10	175.11
$\psi(\text{transloc}), \gamma(0), \varepsilon(0), p(\text{year})$	196.66	11.38	0.001	5	186.66
$\psi(\text{transloc}, \text{park}), \gamma(0), \varepsilon(0), p(\text{year})$	196.84	11.55	0.001	6	184.84
$\psi(\text{transloc}, \text{nrbound}), \gamma(0), \varepsilon(\text{nrbound}), p(\text{year})$	197.62	12.34	0.000	8	181.62

$\psi(\text{nrbound}, \text{park}), \gamma(\text{network}), \varepsilon(0), p(\text{year})$	198.30	13.02	0.000	8	182.30
$\psi(\text{transloc}), \gamma(0), \varepsilon(\text{nrbound}), p(\text{year})$	198.43	13.14	0.000	7	184.43
$\psi(\text{transloc}, \text{park}), \gamma(0), \varepsilon(\text{nrbound}), p(\text{year})$	198.58	13.30	0.000	8	182.58
$\psi(\text{park}), \gamma(\text{network}), \varepsilon(.), p(\text{year})$	199.49	14.21	0.000	8	183.49
$\psi(\text{nrbound}), \gamma(.), \varepsilon(.), p(\text{year})$	199.83	14.55	0.000	7	185.83
$\psi(\text{nrbound}, \text{park}), \gamma(0), \varepsilon(0), p(\text{year})$	200.01	14.73	0.000	6	188.01
$\psi(\text{nrbound}, \text{park}), \gamma(\text{network}), \varepsilon(.), p(\text{year})$	200.30	15.02	0.000	9	182.30
$\psi(\text{park}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{year})$	200.34	15.06	0.000	9	182.34
$\psi(\text{park}), \gamma(0), \varepsilon(0), p(\text{year})$	200.42	15.13	0.000	5	190.42
$\psi(\text{park}), \gamma(.), \varepsilon(.), p(\text{year})$	201.15	15.86	0.000	7	187.15
$\psi(\text{nrbound}, \text{park}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{year})$	201.34	16.06	0.000	10	181.34
$\psi(\text{park}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{year})$	201.49	16.20	0.000	9	183.49
$\psi(\text{park}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{year})$	201.73	16.45	0.000	8	185.73
$\psi(\text{nrbound}, \text{park}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{year})$	202.30	17.02	0.000	10	182.30
$\psi(\text{park}), \gamma(0), \varepsilon(\text{bnd}, \text{rd}), p(\text{year})$	202.42	17.13	0.000	7	188.42
$\psi(\text{nrbound}, \text{park}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{year})$	202.49	17.21	0.000	9	184.49
$\psi(\text{park}), \gamma(\text{year}), \varepsilon(\text{nrbound}), p(\text{year})$	203.29	18.00	0.000	9	185.29
$\psi(\text{nrbound}, \text{park}), \gamma(\text{year}), \varepsilon(\text{nrbound}), p(\text{year})$	203.86	18.58	0.000	10	183.86
$\psi(\text{park}), \gamma(\text{network}), \varepsilon(0), p(\text{year})$	204.42	19.13	0.000	7	190.42
$\psi(\text{park}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{year})$	204.83	19.54	0.000	9	186.83
$\psi(\text{nrbound}, \text{park}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{year})$	204.91	19.63	0.000	10	184.91
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{year})$	188.78	3.49		10	168.78
$\psi(\text{transloc}, \text{park}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{year})$	190.12	4.84		10	170.12

Eurycea bislineata

Model	AIC	Δ AIC	w	K	-2l
$\psi(\text{nrbound}, \text{park}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{year})$	277.80	0.00	0.278	10	257.80
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{network}), \varepsilon(.), p(\text{year})$	278.63	0.83	0.183	9	260.63
$\psi(\text{transloc}, \text{park}), \gamma(\text{network}), \varepsilon(.), p(\text{year})$	279.91	2.11	0.097	9	261.91
$\psi(\text{transloc}, \text{nrbound}), g \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{year})$	280.59	2.79	0.069	10	260.59
$\psi(\text{nrbound}, \text{park}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{year})$	281.82	4.02	0.037	10	261.82
$\psi(\text{park}), \gamma(0), \varepsilon(\text{nrbound}), p(\text{year})$	281.98	4.18	0.034	7	267.98
$\psi(\text{park}), \gamma(.), \varepsilon(.), p(\text{year})$	282.02	4.22	0.034	7	268.02
$\psi(\text{nrbound}, \text{park}), \gamma(\text{year}), \varepsilon(\text{nrbound}), p(\text{year})$	282.08	4.28	0.033	10	262.08
$\psi(\text{transloc}, \text{nrbound}), \gamma(0), \varepsilon(\text{nrbound}), p(\text{year})$	282.36	4.56	0.028	8	266.36
$\psi(\text{transloc}, \text{nrbound}), \gamma(.), \varepsilon(.), p(\text{year})$	282.38	4.58	0.028	8	266.38
$\psi(\text{nrbound}, \text{park}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{year})$	283.02	5.22	0.020	9	265.02
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{year})$	283.29	5.49	0.018	9	265.29
$\psi(\text{park}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{year})$	283.66	5.86	0.015	9	265.66
$\psi(\text{transloc}), \gamma(0), \varepsilon(\text{nrbound}), p(\text{year})$	283.67	5.87	0.015	7	269.67
$\psi(\text{transloc}), \gamma(.), \varepsilon(.), p(\text{year})$	283.70	5.90	0.015	7	269.70
$\psi(\text{transloc}, \text{park}), \gamma(0), \varepsilon(\text{nrbound}), p(\text{year})$	283.98	6.18	0.013	8	267.98
$\psi(\text{park}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{year})$	283.98	6.18	0.013	8	267.98
$\psi(\text{transloc}, \text{park}), \gamma(.), \varepsilon(.), p(\text{year})$	284.02	6.22	0.012	8	268.02
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{year}), \varepsilon(\text{nrbound}), p(\text{year})$	284.35	6.55	0.010	10	264.35
$\psi(\text{psi}(\text{transloc}, \text{nrbound}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{year}))$	284.36	6.56	0.010	9	266.36
$\psi(\text{transloc}, \text{park}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{year})$	285.33	7.53	0.006	10	265.33
$\psi(\text{psi}(\text{transloc}, \text{nrbound}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{year}, \text{month}))$	285.59	7.79	0.006	10	265.59
$\psi(\text{transloc}, \text{park}), \gamma(\text{year}), \varepsilon(\text{nrbound}), p(\text{year})$	285.60	7.80	0.006	10	265.60
$\psi(\text{transloc}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{year})$	285.67	7.87	0.005	8	269.67
$\psi(\text{transloc}, \text{park}), \gamma(.), \varepsilon(\text{nrbound}), p(\text{year})$	285.98	8.18	0.005	9	267.98
$\psi(\text{transloc}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{year})$	286.77	8.97	0.003	9	268.77
$\psi(\text{transloc}), \gamma(\text{year}), \varepsilon(\text{nrbound}), p(\text{year})$	287.06	9.26	0.003	9	269.06
$\psi(\text{park}), \gamma(\text{network}), \varepsilon(0), p(\text{year})$	288.44	10.64	0.001	7	274.44
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{network}), \varepsilon(0), p(\text{year})$	288.97	11.17	0.001	8	272.97
$\psi(\text{transloc}, \text{nrbound}), \gamma(.), \varepsilon(\text{nrbound}), p(.)$	289.25	11.45	0.001	7	275.25
$\psi(\text{transloc}, \text{park}), \gamma(\text{network}), \varepsilon(0), p(\text{year})$	290.24	12.44	0.001	8	274.24
$\psi(\text{psi}(\text{transloc}, \text{nrbound}), \gamma(.), \varepsilon \text{ nrbound}), p(\text{month})$	290.42	12.62	0.001	8	274.42
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(0), p(\text{year})$	292.16	14.36	0.000	7	278.16
$\psi(\text{park}, \text{nrbound}), \gamma(0), \varepsilon(0), p(\text{year})$	293.47	15.67	0.000	6	281.47
$\psi(\text{park}), \gamma(0), \varepsilon(0), p(\text{year})$	294.06	16.26	0.000	5	284.06
$\psi(\text{transloc}, \text{nrbound}), \gamma(0), \varepsilon(0), p(\text{year})$	294.32	16.52	0.000	6	282.32
$\psi(\text{transloc}), \gamma(0), \varepsilon(0), p(\text{year})$	295.75	17.95	0.000	5	285.75
$\psi(\text{transloc}, \text{park}), \gamma(0), \varepsilon(0), p(\text{year})$	296.06	18.26	0.000	6	284.06
$\psi(\text{nrbound}, \text{park}), \gamma(\text{network}), \varepsilon(.), p(\text{year})$	276.16			9	258.16
$\psi(\text{nrbound}), \gamma(\text{network}), \varepsilon(.), p(\text{year})$	277.02			8	261.02

$\psi(\text{park}, \text{nrbound}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{year})$	278.11	10	258.11
$\psi(\text{park}), \gamma(\text{network}), \varepsilon(.), p(\text{year})$	278.12	8	262.12
$\psi(\text{park}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{year})$	279.76	9	261.76
$\psi(\text{park}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{year})$	280.06	9	262.06
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{year})$	280.27	10	260.27
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{year})$	280.59	10	260.59
$\psi(\text{nrbound}, \text{park}), \gamma(.), \varepsilon(.), p(\text{year})$	281.06	8	265.06
$\psi(\text{park}, \text{nrbound}), \gamma(0), \varepsilon(\text{nrbound}), p(\text{year})$	281.51	8	265.51
$\psi(\text{transloc}, \text{park}), \gamma(\text{network}), \varepsilon(\text{year}), p(\text{year})$	281.54	10	261.54
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(.), p(\text{year})$	281.64	8	265.64
$\psi(\text{transloc}, \text{park}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{year})$	281.86	10	261.86
$\psi(\text{transloc}), \gamma(\text{network}), \varepsilon(\text{nrbound}), p(\text{year})$	283.60	9	265.60
$\psi(\text{transloc}, \text{nrbound}), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{year})$	284.07	10	264.07
$\psi(\text{park}, \text{nrbound}), \gamma(\text{network}), \varepsilon(0), p(\text{year})$	286.34	8	270.34

Table 11. Model averaged initial occupancy estimates $\hat{\psi}_{2005}$ for 3 stream salamander species at Chesapeake and Ohio NHP(CHOH) and Rock Creek Park(ROCR). Reported are model-averaged $\hat{\psi}_{2005}$ estimates for paired transects: at the stream origin(Upper), 145m from the stream origin(Lower), within streams that originate near a park boundary or road(Near), or within streams that originate well within park boundaries(Far). Estimates were calculated using models whose summed weights were ≥ 0.95 (see Table 10). Model averaged estimates do not include models investigated *a posteriori*, nor those used to investigate covariate structure on detection probability.

		CHOH		ROCR	
Transect location		Upper	Lower	Upper	Lower
<i>Desmognathus fuscus</i>	Model-averaged ψ	0.79	0.54	0.28	0.10
	Unconditional SE	0.17	0.31	0.28	0.14
<i>Pseudotriton ruber</i>	Model-averaged ψ	0.68	0.00	0.58	0.00
	Unconditional SE	0.27	-	0.33	-
<i>Eurycea bislineata</i>	Model-averaged ψ	0.73	0.80	0.90	0.96
	Unconditional SE	0.40	0.44	0.46	0.47

		CHOH		ROCR	
Stream location		Near	Far	Near	Far
<i>Desmognathus fuscus</i>	Model-averaged ψ	0.81	0.79	0.31	0.28
	Unconditional SE	0.16	0.18	0.30	0.28
<i>Pseudotriton ruber</i>	Model-averaged ψ	0.63	0.68	0.55	0.60
	Unconditional SE	0.30	0.27	0.34	0.33
<i>Eurycea bislineata</i>	Model-averaged ψ	1.00	0.73	1.00	0.90
	Unconditional SE	-	0.40	-	0.46

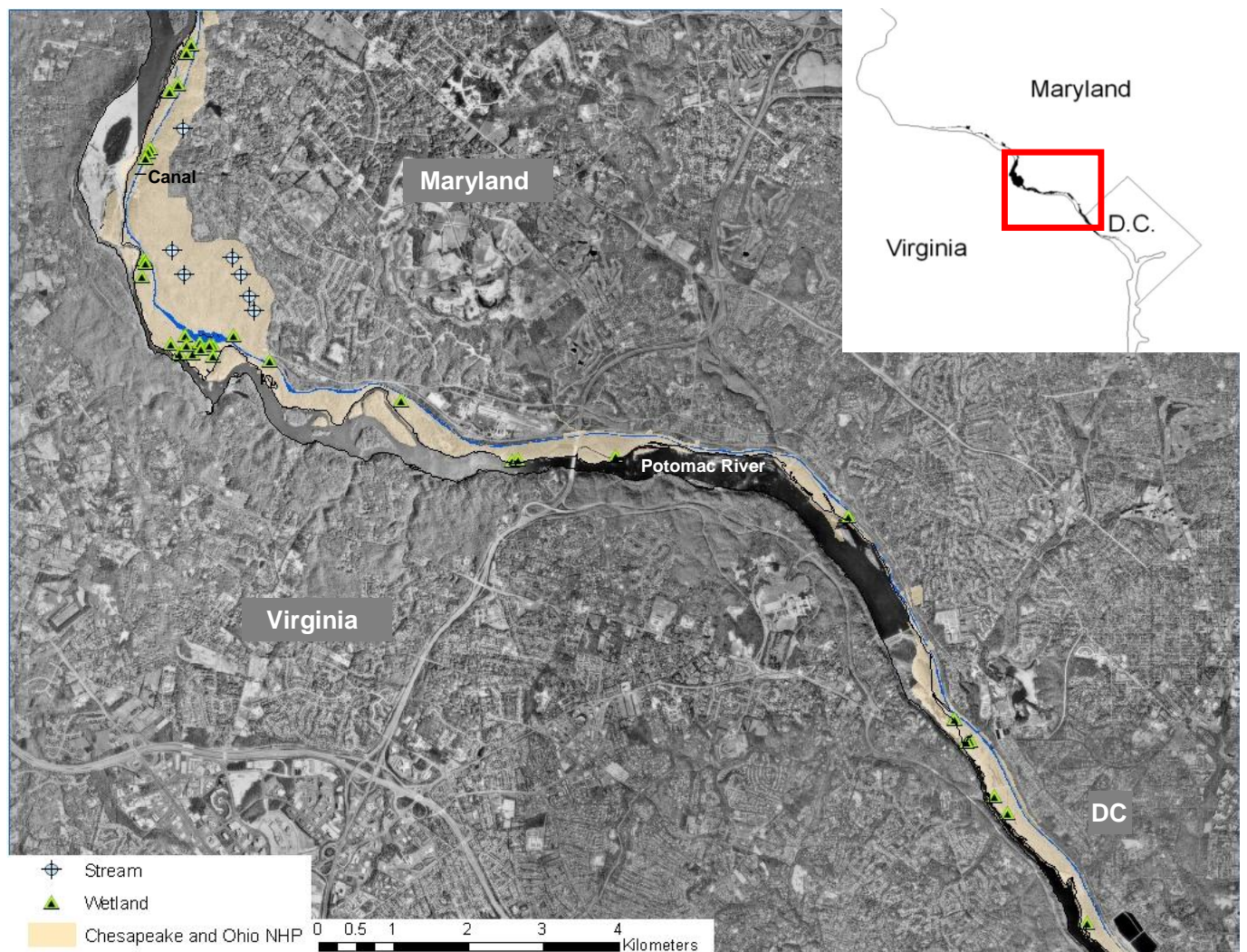


Figure 1. Study area: location of the 33 wetlands and 7 streams surveyed for amphibians in the Chesapeake and Ohio NHP(2005-2007).

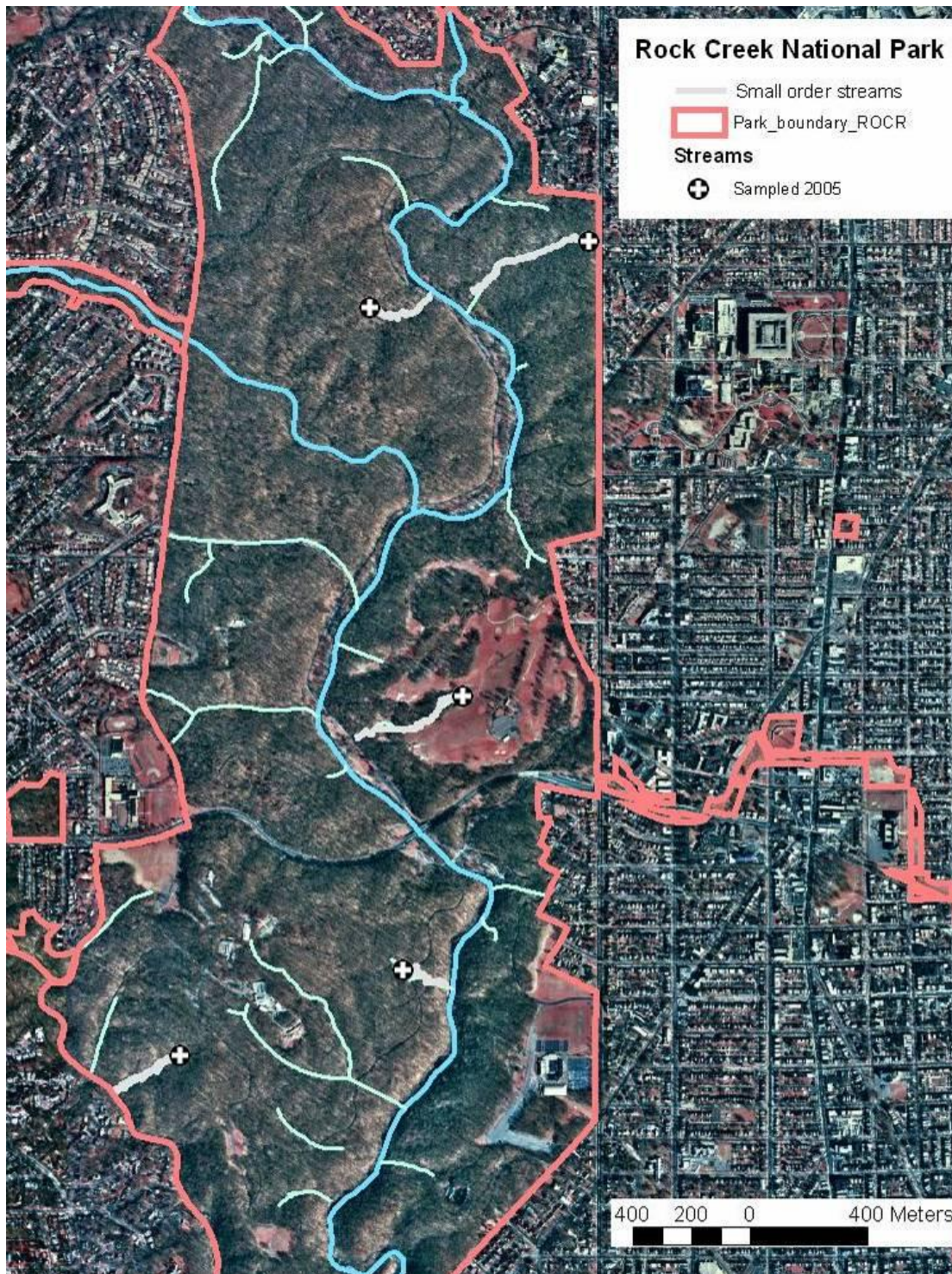


Figure 2. Study area: location of the 5 streams surveyed for amphibians in Rock Creek Park(2005-2007).

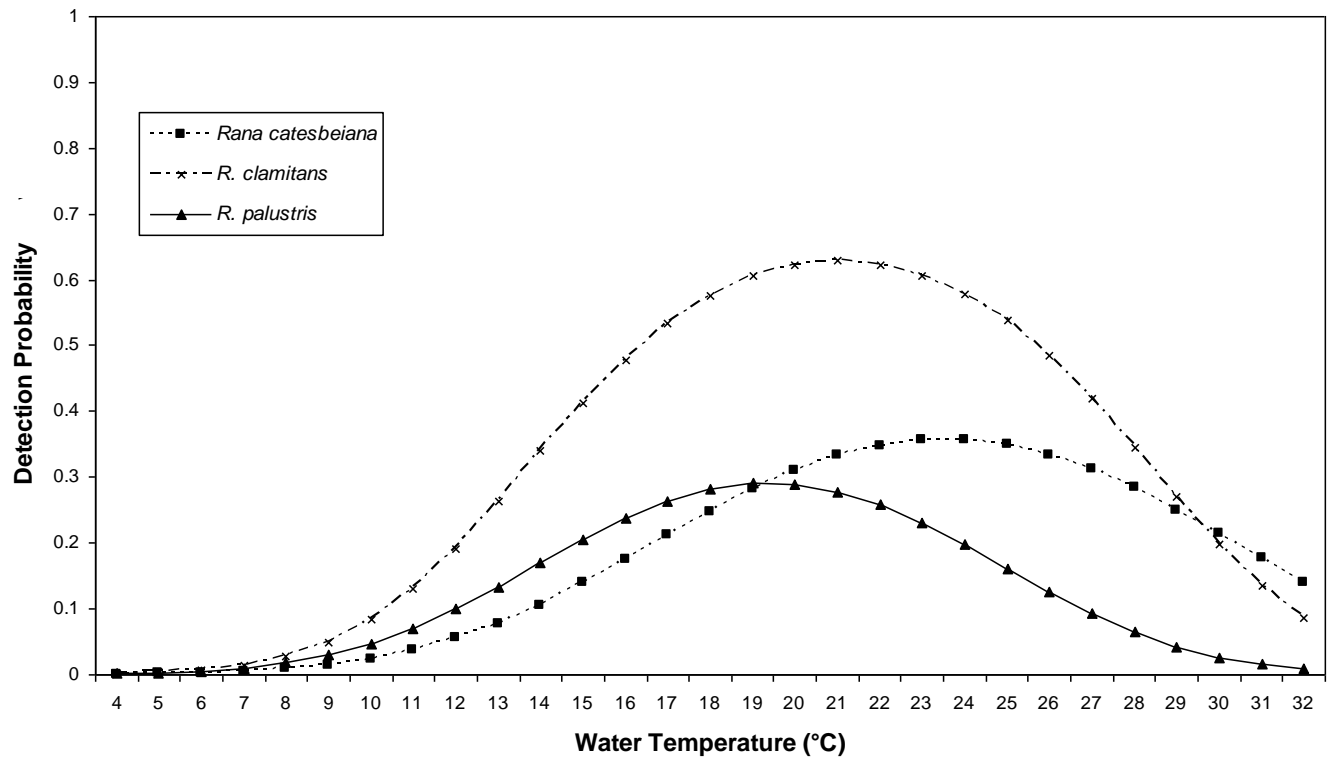


Figure 3. The relationship between the detection probability and water temperature for 3 amphibian species(*Rana catesbeiana*, *R. clamitans* and *R. palustris*) at wetlands in the Chesapeake and Ohio NHP.

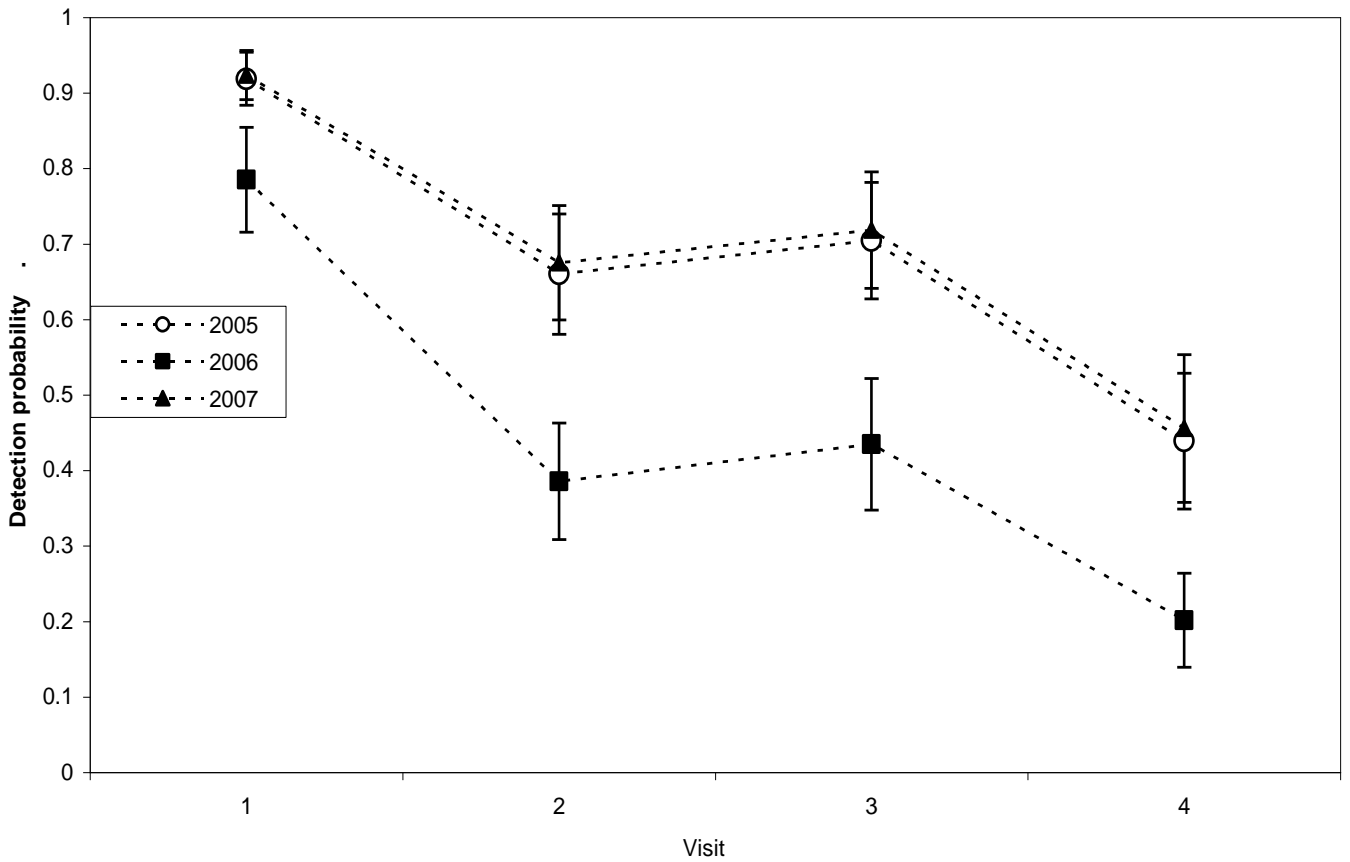


Figure 4. The relationship between the detection probability of *Ambystoma maculatum* and visit(1-4) for each year(2005-2007) at wetlands in the Chesapeake and Ohio NHP. Error bars represent ± 1 SE.

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NPS D-XXX, January 2008

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